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Structure and organization of canopy bird assemblages in lowland neotropical rainforests

David Lawrence Anderson
Louisiana State University and Agricultural and Mechanical College, danders@tigers.lsu.edu

STRUCTURE AND ORGANIZATION OF CANOPY BIRD ASSEMBLAGES IN LOWLAND NEOTROPICAL RAINFORESTS

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David Lawrence Anderson
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M.S., Boise State University, 1998
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ABSTRACT

Although birds of the forest canopy are an important component of tropical forest ecosystems, difficulty accessing the forest canopy has limited the advancement of knowledge pertaining to this group of species. Here I test methods for the study of canopy birds in lowland Neotropical rainforests, and identify recurring patterns of community structure in canopy bird assemblages as well as processes potentially responsible for these patterns.

I used three methods to assess differences in ground-based and canopy-based methods for detecting forest birds in a 100-ha plot of lowland rainforest in northern Honduras: (1) point counts from the ground; (2) repeat censuses from two canopy trees; and (3) single censuses from multiple canopy trees. Ground methods significantly underestimated species and familial richness as well as abundances of individuals in the canopy stratum, and I predict that ground methods miss 25 to 50% of the species richness for some migrant and resident families and underestimates the density of some species by as much as 25%.

I compared two distant canopy bird assemblages based on >11,000 detections at lowland rainforest sites in Honduras and Amazonian Brazil. Richness of canopy birds was similar between sites, despite overall higher forest bird richness in Brazil. Honduras and Brazil differed significantly in abundance distributions, with greater evenness characterizing the Brazil assemblage. Long-distance migrants and species of forest edges and open habitats were underrepresented at both sites when compared to null expectations drawn from regional species pools. Long-distance migrants were relatively more important in Honduras, where they constituted a third of canopy birds. Species richness of omnivores amongst core canopy species was greater than expected at both sites, and omnivores dominated the canopy in terms of species richness and individual abundance.

Functional morphology analyses indicated that core canopy birds are more similar phenotypically than would be expected by chance. Similarity in functional morphology may result from environmental filtering selecting for phenotypes optimally suited for survival in the harsh canopy environment. Phylogeny seems to be an important underlying component of morphological similarity, however, and may exert a structuring force on the canopy bird assemblage through phylogenetic niche conservatism.

CHAPTER 1: INTRODUCTION

While the field of tropical ecology has evolved steadily from a descriptive science to rigorous hypothesis testing, the difficulty of accessing the forest canopy has slowed similar advances in ecological methods and theory for the upper portion of forests that remains largely out of reach and out of sight (Lowman and Rinker 2004). As human actions continue to affect biodiversity in tropical forests, our ability to preserve the diversity that remains will depend on improving our awareness of patterns of diversity and knowledge on the processes that create and maintain diversity at all levels of the forest ecosystem. Advancing our knowledge on such a complex array of processes in canopy biology, however, must first depend on improving current methods for studying canopy organisms and the identification of relevant patterns of diversity.

For my dissertation, I examined the structure and organization of avian assemblages that inhabit the canopy of lowland Neotropical rainforests. I designed the dissertation to address avian biology in forest canopies at three levels of importance: 1) analyze the efficacy of and improve upon current methods for censusing canopy birds; 2) use canopy-based methods to draw inferences on patterns of diversity and organization of avian assemblages in forest canopies; and 3) examine deterministic processes that shape the organization of canopy bird assemblages.

Methods research is fundamental to applied ecology and conservation, because much of applied ecology involves counting organisms and deriving ecological inference from such counts (Elphick 2008). In tall and structurally complex tropical forests, a ground-based observer is separated from birds by distances of 30 to more than 60 m and by dense vegetation, both of which will affect the detection of birds, estimates of their population density, and inferences on the ecology of forest birds and the larger forest ecosystem (Bibby et al. 2000a, Pacifici et al. 2008). In my chapter 2 I compare results from traditional point-count transects conducted on the ground to those from two census methods conducted from the canopy. This design allowed an

empirical quantification of the bias associated with ground-based methods for canopy birds, and the development of recommendations of more robust census methods for this group.

Despite pioneering studies on canopy bird assemblages (Greenberg 1981, Loiselle 1988, Naka 2004) fundamental issues on their structure and organization have remained unresolved, such as trophic organization, and the relative importance of habitat generalists and long-distance migrants in the canopy. In Chapter 3 I take a comparative approach and examine the structure and composition of canopy bird assemblages at distant sites in Honduras and Brazil. By comparing two lowland rainforest sites censused with similar canopy-based methods and sharing similar climate, elevation, and forest structure, yet differing in biogeographic history, I was able to empirically address these previously unresolved issues.

In Chapter 4 I address a foundational question in ecology, namely why some species in a larger region become members of a local community whereas others do not. I use morphometrics and the study of functional morphology to make inferences on community assembly and the importance of deterministic ecological processes in shaping the structure of the ensemble of avian insectivores observed in the canopy of my Honduras study site.

CHAPTER 2: GROUND VERSUS CANOPY METHODS FOR THE STUDY OF BIRDS IN TROPICAL FOREST CANOPIES: IMPLICATIONS FOR ECOLOGY AND CONSERVATION[1]

INTRODUCTION

As the rapid pace of tropical deforestation continues, improving our understanding of the processes that create and maintain forest biodiversity is increasingly essential for the continued preservation of the forests that remain (Millennium Ecosystem Assessment 2005). This understanding, in turn, is directly tied to the quality and variety of methods used to observe and study both processes and diversity. In tall and structurally complex tropical forests, a complete understanding of forest ecosystems must address diversity and ecological interactions at all levels of the forest (Lowman and Rinker 2004). Development of field methods for the study of forest canopies, however, has been hindered by the difficulty of gaining access or seeing into the forest canopy.

Birds are a conspicuous and important component of tropical forest ecosystems. Canopy bird communities include important functional groups, such as seed dispersers, pollinators, and top predators (Howe 1977, Nadkarni and Matelson 1989, Blake and Loiselle 2000, Holbrook and Smith 2000, Anderson 2001). Long-distance and elevational migrants also occur in the canopy, and their conservation requires an understanding of their ecology, distribution, and abundance (Loiselle 1987, Powell and Bjork 1995, Chaves-Campos et al. 2003). Of further conservation concern is the suggestion that canopy bird species may be disproportionately sensitive to forest fragmentation (Castelletta et al. 2000, Robinson et al. 2000, Sodhi et al. 2004), and several canopy species (e.g., large raptors, macaws, and some frugivores) are threatened or endangered in Middle America (Terborgh and Winter 1980, Kattan 1992, Levey and Stiles 1994). It follows

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that the conservation of tropical forests will depend in part on an accurate appreciation of canopy birds and their interactions within the forest ecosystem.

One of the methods used most frequently to study the abundance, distribution, and ecology of forest birds is the point count (Ralph et al. 1995). Point-count data are used to make inferences about the presence and abundance of birds, but an important consideration of this method is the probability of the birds' detection (Farnsworth et al. 2002), which can vary widely with species, habitat, and time of day or year, among other factors (Blake 1992, Ralph et al. 1995, Pacifici et al. 2008). The ability of an observer on the ground to detect birds in a tropical forest canopy varies dramatically because of (1) the range of conspicuousness of different species depending on size, coloration, vocalizations, and movements and (2) the dense foliage and distance that separate the observer from the canopy (Pacifici et al. 2008). In short, some canopy species should be harder to detect from the ground, in particular those that have soft vocalizations, call infrequently, or remain perched for long periods of time. The difficulty of detecting such species has led to the conclusion that canopy species are likely underrepresented in otherwise comprehensive studies of Neotropical forest bird assemblages that rely on ground-based sampling (Robinson et al. 2000, Blake 2007).

A few pioneering studies have advanced methods for studying birds in Neotropical forest canopies (Greenberg 1981, Loiselle 1988, Naka 2004). Despite such advances, no attempt has been made to quantify the differences between ground-based and canopy-based data on canopy birds. Because of the continued reliance on ground-based methods, such a comparison is crucial to assessing their value for the study of canopy birds and to determine what biases or limitations may exist. Any substantial weaknesses that are revealed could have major implications for the understanding of forest bird communities, ecosystem processes, and the conservation of both.

The major goal of this study was to address the basic question of the relative validity of ground-based methods for the study of canopy birds. Therefore, I compared the results of ground point counts and two types of canopy point counts in a 100-ha plot in northern Honduras sampled over a complete annual cycle. To my knowledge, this study is the first to make such a comparison and the first to use canopy-based methods to sample canopy birds in a 100-ha plot. A quantitative definition of what constitutes a "canopy bird species" has remained elusive but should prove useful in discussions of canopy bird ecology and conservation. To compare canopy and noncanopy birds, I combined the data sets to define quantitatively the core canopy species of the study area. I then compared patterns of species richness, as well as family and species composition, as represented by the respective data sets derived from the three methods. Finally, I compared detection rates of canopy birds as a whole and of groups of quieter or less conspicuous species that I suspected would be underrepresented in ground-based data sets.

METHODS

Study Area

I delineated a 100-ha study site (15º 43.40′ N, 86º 44.08′ W) in the Río Cangrejal valley on the humid north flank of Pico Bonito National Park, Honduras. The park encompasses 107,090 ha and elevations ranging from 50 to 2480 m (FUPNAPIB 2004). A majority of the park is primary forest with no recent history of human disturbance. Annual precipitation and mean temperature for the site are 2900 mm and 26°C, respectively. The wet and dry seasons are distinct: the driest months are April and May with an average monthly rainfall of 89 mm; the wettest months are November and December with an average monthly rainfall of 510 mm (FUPNAPIB 2004).

Slopes in the study area are nearly flat to moderately steep, and elevations range from 100 to 350 m. The forest averages 35–40 m high, and canopy emergents are rare. Primary and mature secondary moist forests are both present, with primary forests constituting about 60% of the study area. Common overstory tree species include *Symphonia globulifera*, *Vochysia guatemalensis*, *Virola koschnyi*, *Tapipira guianensis*, *Astronium graveolens*, *Bursera simaruba*, *Pouteria* spp., *Ficus* spp., *Calophyllum brasiliense, Dialium guianensis,* and *Schizolobium parahybum*. Numerous wind-snapped trees, gaps, and canopy vine tangles suggest a high incidence of weather-related disturbance.

Sampling Methods

I tested three methods, one ground-based and two canopy-based, for their effectiveness in detecting canopy birds. The first method (henceforth ground) used point transects located along pre-existing trails. I established 30 count stations along two trails that bisected the study area. Stations were separated by 100 m. This spacing was chosen because many Neotropical species are hard to hear at distances >30 m (Terborgh et al. 1990, Robinson et al. 2000, Blake 2007). Censuses started 30 min after sunrise and typically lasted 3 hours, during which I normally covered approximately 1.3 km and 13 points. I selected the starting time to standardize sampling times with canopy censuses (see below). I rotated starting points to ensure, as much as possible, that all points were covered early in the morning when vocal activity was greatest. I conducted counts on days with no rain and little or no wind and terminated counts when rain or wind interfered with the detection of birds. I counted birds for 10 min at each point. Any individual detected from more than one point was noted as such, but only the first detection was used in analyses. The maximum number of individuals per species, summed for all points of a given census walk, was the datum used in analyses.

For the second method (repeat-tree method), I conducted repeat censuses from the crowns of two trees, a method similar to that of previous canopy-bird studies (Greenberg 1981, Loiselle 1988, Naka 2004). The first tree was a 45-m tall *Vochysia guatemalensis* in mature secondary forest at 115 m. The second tree was a 60-m tall *Virola koschnyi* in primary forest at 220 m. The trees were separated by 1 km. I conducted 22 censuses from these two trees. For the third method (single-tree method), I conducted single censuses from the crowns of 22 separate trees interspersed throughout the entire study area. I used a crossbow and single-rope technique to climb canopy trees (Sillett and Van Pelt 2000). I selected census trees on the criteria that they were safe to climb, had an open crown structure that allowed views out of the census tree, and were a minimum of 50 m from other census trees. Census trees closer than 100 m to each other were censused in different seasons (see below).

All canopy censuses began 30 min after sunrise and lasted 3 hours. Following the protocol of Loiselle (1988) and Naka (2004), I further subdivided the 3-hr censuses into 12 consecutive 15-min intervals. The use of short intervals facilitates tracking individual birds, which can be distinguished by differences in plumage and location in the forest, and avoids double counting (i.e., it is easier to follow individual birds and their direction of travel over a 15-min period than over 3 hr). The maximum number of individuals per species within a 15-min period was used for analysis of census results, unless additional individuals were identified on the basis of sex or plumage. Canopy census plots had a radius of 150 m and an area of 7.1 ha. Additionally, both repeat trees and eight single trees were paired with count points on the ground.

I recorded all birds seen or heard and categorized them into one of four forest strata: (1) *ground* (soil, leaf litter, and fallen logs), (2) *understory* (the space from the ground to 2 m), (3)

midstory (the space between the understory and canopy), and (4) *canopy* (the sum of all tree crowns exposed to the sky above; Bongers 2001, Fig. 1C). Birds flying over the forest were noted as such and excluded from analyses. Finally, I noted for every observation whether the initial detection cue was by sight or sound.

I sampled birds over a complete annual cycle from April 2006 to April 2007. I subdivided the year into four seasons—early and late dry, and early and late wet—to compare seasonal variation in species abundance. This technique has been used in previous studies of Neotropical forest birds (Greenberg 1981, Loiselle 1987, 1988, Blake 1992) to account for changes in forest phenology, principally the development and abundance of certain resources used by birds or their prey (e.g., flowers, nectar, fruit, insects, and leaves) that may affect the seasonal abundance and distributions of birds. Furthermore, seasonal changes in leaf density caused by leaf fall and regeneration, as well as natural levels of background noise, particularly cicadas, can affect the detectability of birds (Pacifici et al. 2008).

Statistical Analyses

Because of differences in the spatial distribution, size, and number of plots used in each method, I do not attempt to estimate densities of species detected by each method. Rather, I present numbers of individual detections (by sight or sound) per method. This conservative approach focuses on the ability of each method to detect species and individuals in the canopy rather than to describe the canopy-bird community *per se* and is in line with the scope of the current study.

I used the method of Neu et al. (1974) to quantify birds' preference for the canopy stratum. I established 95% confidence limits, based on Bonferroni's adjustment of the significance level, around the observed frequency of detection in the canopy stratum for species

with ≥4 detections. A significant preference for the canopy was indicated by expected values below the 95% confidence limits for the observed values (Haney and Solow 1992, Cardoso da Silva et al. 1996). I refer to species that met this criterion as core canopy species. I excluded from analyses nocturnal species and birds flying over the forest. Taxonomy follows AOU (1998) and supplements.

I used rarefaction analyses to compare rates of species accumulation among the three methods. Rarefaction curves are produced by repeatedly and randomly resampling the pool of observations and plotting the average number of species represented by *n* individuals; they are therefore a statistical representation of species-accumulation curves (Gotelli and Colwell 2001, Magurran 2004a). I used Chao 1 and Chao 2 nonparametric estimators (Magurran 2004b) to estimate species richness from each method. These analyses were conducted with EstimateS version 7.5 (Colwell 2005).

I followed the methods of Pitman et al. (2001) and Blake (2007) to compare the number of detections per family. This method tests the null hypothesis that the three methods are equivalent in terms of species or family composition. If two methods are equivalent in the number of detections, then the slope of the regression line should be equal to 1 (Blake 2007). I used two subtly different approaches to compare my ability to detect canopy birds with each census method: (1) the hourly detection rate of all species and individuals in the canopy stratum and (2) the hourly detection rate of core canopy species and individuals in all forest strata. The first approach addresses the question, "are the methods equal in their ability to detect birds in the canopy?" The second approach addresses a different question, "are the methods equal in their ability to detect those species that spend a substantial portion of their time in the forest canopy?" I used mixed-model ANOVA to control for the effects of season and forest type and to test for an

effect of method on the hourly detection rates of species and individuals. Data were first square-root transformed to meet assumptions of normality. I used post hoc Tukey's pairwise comparisons to test for significant differences between pairs of methods.

I used a two-step method to test for an effect of method on the hourly detection rates of three groups of inconspicuous canopy species, namely, (1) inconspicuous residents with soft or infrequent vocalizations, (2) inconspicuous migrants, and (3) canopy hummingbirds. For each group I considered only those species that qualified as core canopy species and compared the detection rate on the basis of all individuals within each group that were detected in any stratum. To test for differences, I first used a Kruskal–Wallis test to test for an overall effect of method on detection rates for each group. Upon finding a significant effect of method, I then used a Wilcoxon signed-rank test to make pairwise comparisons between methods. I used this same approach to test for differences between detection rates of highly vocal and conspicuous canopy species. All statistical tests were assumed significant at $P < 0.05$.

RESULTS

Numbers of Detections and Species

I conducted a total of 71 censuses from April 2006 to April 2007, resulting in 4613 individual detections of 157 species, 112 of which I observed in the canopy (Table 2.1). I recorded an additional 27 species outside standardized surveys but excluded these from analyses. Sixty-five species (60% of all species detected in the canopy) qualified as core canopy species. Species-rarefaction curves for all species suggest that most species on the plot were detected by the combination of methods but that sampling by any single method was less complete (Fig. 2.1a). Curves for detections in the canopy stratum do not reach asymptotes, suggesting that some species observed in lower strata would eventually be encountered in the canopy stratum

TABLE 2.1 Number of species and detections (by sight or sound) by three census methods in 100 ha near the Río Cangrejal, Pico Bonito National Park, Honduras.

			Number of species/number of detections			
			All species		Core canopy species	
Method	Censuses	Census hours	All strata	Canopy stratum	All strata	Canopy stratum
Ground	27	66.7 (2.4±0.56)	110/1824	36/300	47/986	31/329
Repeat-tree	22	66 (3.0±0)	121/1598	91/936	64/1149	64/900
Single-tree	22	66 (3.0±0)	123/1191	96/675	59/863	59/614
Total	71	198.7	157/4613	112/1911	65/2998	65/1843

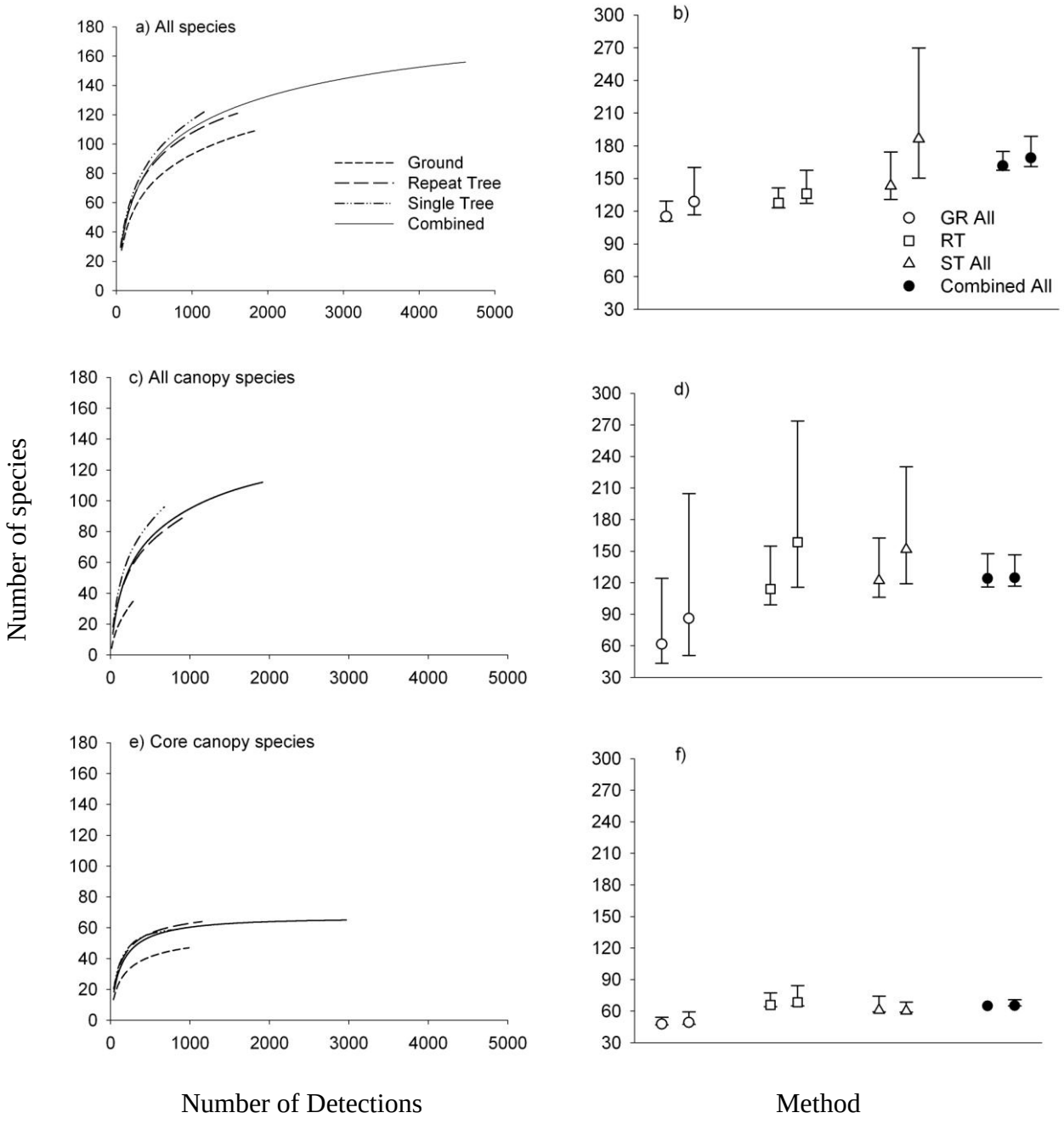


FIGURE 2.1 Sample-based rarefaction curves (left column) and corresponding estimates of species richness (right column) for three census methods and the combined data set, Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Each pair of cells depicts all detections of all species (a, b), canopy detections of all species (c, d), and all detections of core canopy species (e, f). Each duo in b, d, and f corresponds to richness estimates from Chao 1 and Chao 2 estimators, respectively. Shapes and vertical bars represent means and 95% confidence intervals, respectively.

(Fig. 2.1c). Sampling of core canopy species was more complete, with all curves quickly reaching asymptotes (Fig. 2.1e). The actual number of species estimated for the study area by the combined data set lies between 162 and 189, not significantly greater than the 156 actually observed (Fig. 2.1b). Richness estimates for core canopy species by the canopy methods and the combined data set did not differ, but all three of these estimates were significantly higher than those derived from ground censuses (Fig. 2.1f). Repeat-tree and single-tree censuses detected nearly the full complement of core canopy species, whereas the ground censuses detected only 47 (72%) of all core canopy species. On the basis of the level of sampling I achieved, richness estimates for all canopy species did not differ regardless of census method (Fig. 2.1d).

Distributions of abundances of the core canopy species according to canopy and ground censuses differed significantly when comparisons were limited to canopy detections only (Kolmogorov–Smirnov two-sample tests; Fig. 2.2b, Table 2.2). Most of the curve for ground censuses lies below the curves for canopy censuses, indicating (1) larger differences in abundance by species and (2) a greater predominance of common species and an omission of rare ones. These patterns disappear when detections of core canopy species in all strata are considered (Fig. 2.2a, Table 2.2), in which case there were no significant differences between methods.

Family Composition

I observed 27 families in the canopy stratum (Table 2.3). Ground censuses detected eight fewer families in the canopy than repeat-tree censuses and nine fewer families than single-tree censuses. The pattern of species richness per family was the same for the repeat-tree and single-tree methods, as indicated by the slope of the regression being equal to 1.0 (Fig 2.3c). In contrast, the pattern of species richness per family by either canopy method differed significantly

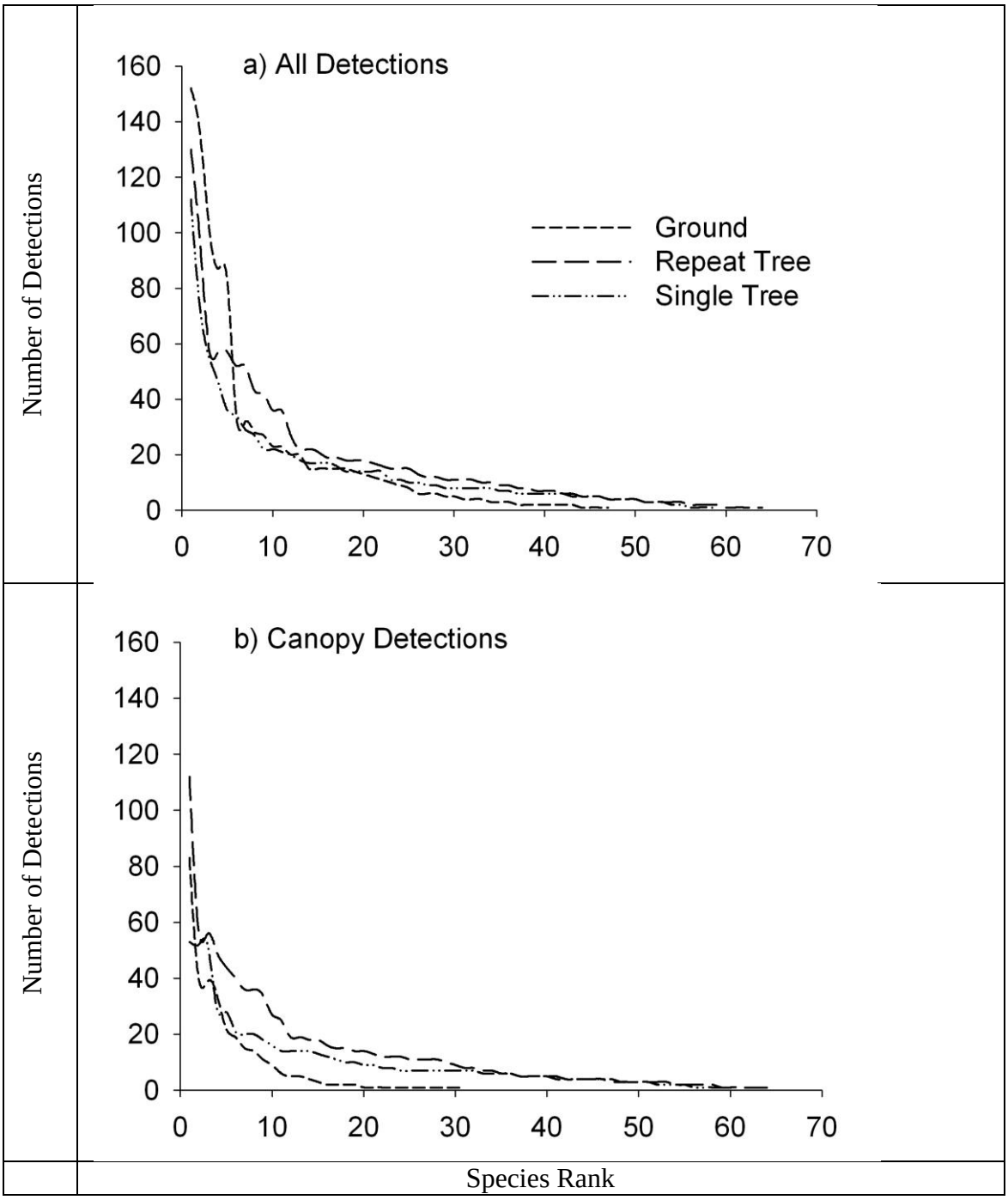


FIGURE 2.2 Rank-abundance curves based on numbers of detections (by sight or sound) of core canopy species in all strata (a) and the canopy stratum only (b) on the 100-ha Río Cangrejal study plot, Pico Bonito National Park, Honduras, April 2006–April 2007.

TABLE 2.2 Kolmogorov–Smirnov two-sample significance tests for differences between survey methods of rank-abundance distributions of core canopy species.

Comparison	KS statistic	*P*
Detections in the canopy stratum		
Ground–repeat-tree	0.16	0.014
Ground–single-tree	0.18	0.006
Repeat-tree–single-tree	0.08	0.489
Detections in all strata		
Ground–repeat-tree	0.05	0.906
Ground–single-tree	0.07	0.638
Repeat-tree–single-tree	0.05	0.904

TABLE 2.3. Numbers of species and individual detections (*n*) by sight or sound in the canopy stratum for each of three census methods at Pico Bonito National Park, Honduras, April 2006 to April 2007.

	Ground		Repeat-tree		Single-tree		Combined	
Family	Spp.	*n*	Spp.	*n*	Spp.	*n*	Spp.	*n*
Cracidae	1	2	0	0	1	1	1	3
Accipitridae	2	2	1	5	2	8	2	15
Columbidae	1	9	3	5	1	4	3	18
Psittacidae	2	50	2	46	3	74	3	170
Cuculidae	0	0	2	16	2	8	2	24
Trochilidae	0	0	9	36	6	34	9	70
Trogonidae	3	4	2	9	4	14	4	27
Momotidae	0	0	1	1	1	2	1	3
Galbulidae	0	0	0	0	1	4	1	4
Bucconidae	0	0	1	2	0	0	1	2
Ramphastidae	2	43	4	90	3	50	4	183
Picidae	1	1	5	26	3	15	5	42
Funariidae[a]	0	0	3	7	5	7	5	14
Thamnophilidae	0	0	2	2	3	8	3	10
Tyrannidae[b]	5	18	16	108	20	94	21	220
Cotingidae	0	0	1	11	1	4	1	15
Pipridae	0	0	1	1	2	3	2	4
Vireonidae	3	89	7	141	7	86	7	316
Corvidae	1	5	1	25	1	12	1	42
Troglodytidae	0	0	1	4	1	7	1	11
Polioptilidae	1	5	2	39	2	33	2	77
Turdidae	1	4	1	3	3	7	3	14
Parulidae	5	8	11	64	8	46	12	118
Thraupidae[c]	3	4	7	99	7	60	8	163
Cardinalidae	1	12	2	50	2	6	2	68
Icteridae	2	41	3	128	4	63	4	232
Fringillidae	2	3	3	18	3	25	4	46
Total families	17		25		26		27	

[a]Includes Dendrocolaptidae.
[b]Includes *Tityra*, *Pachyramphus*, and *Schiffornis.*
[c]Includes *Piranga.*

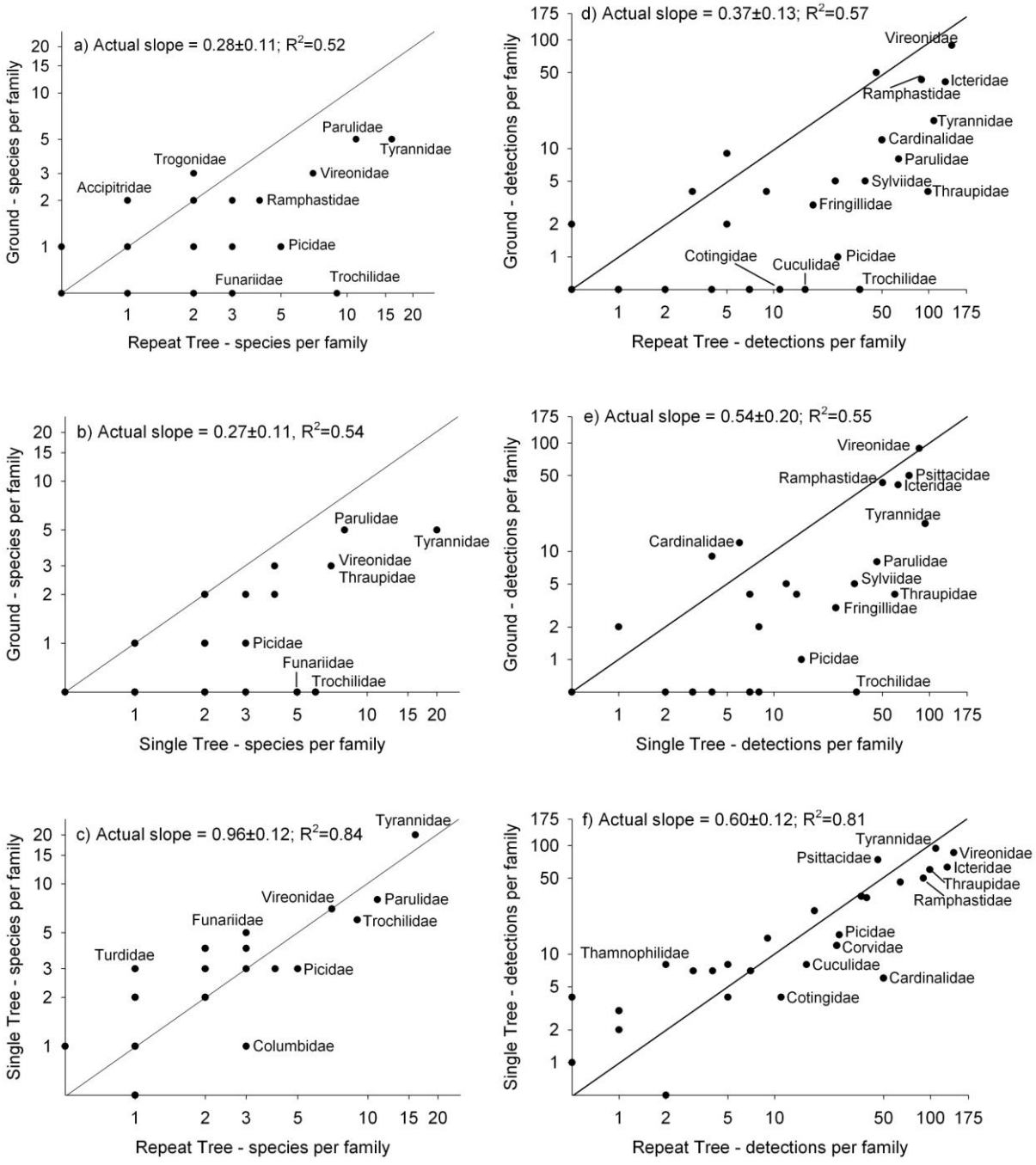


FIGURE 2.3 Number of species (a–c) and detections (by sight or sound; d–f) per family estimated by three census methods in the Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Data represent detections from the canopy stratum only. Straight lines indicate a 1:1 relationship between values for two methods. Actual slopes are given.

from that by the ground method, as indicated by slopes deviating substantially from 1.0 (Fig. 2.3a, b). With only two exceptions, species richness per family was greater for both canopy methods than for the ground method. Patterns of detections per family were less precise, with no relationship between methods approaching a slope of 1.0 (Fig. 2.3d, e, f), although once again the canopy methods were most similar. Substantially more individuals were detected in the canopy during canopy censuses than during point counts from the ground.

Species Composition

I found important differences among dominant species as detected by the three census methods. Eleven of the top 20 species were detected by all three methods, but in no case were species ranked the same in numbers of detections by the three methods (Table 2.4). Species that were more evenly distributed across the study area (e.g., *Hylophilus decurtatus*, *Cyanocorax morio*, *Polioptila plumbea*) or that were highly conspicuous (e.g., *H. decurtatus*, *Ramphastos sulfuratus*, *Psarocolius wagleri*) ranked similarly by all methods. Species that were either less common or less conspicuous (e.g., *Thalurania colombica*, *Piranga rubra*, *Chlorophanes spiza*) tended to rank very differently by different methods. The top 20 species accounted for a greater percentage of canopy observations made from the ground (96%) than they did in canopy observations made from the canopy (76% and 70% for the repeat-tree and single-tree methods, respectively). This pattern signals that fewer species were detected in the canopy during ground censuses and that the evenness of dominant species by this method was also less. This is evident in the inclusion of *Penelope purpurascens*, not characteristically a canopy species, in the list of dominant canopy species for ground censuses.

TABLE 2.4 Percentage of detections and rank for the 20 most frequently detected species in the forest canopy, by method, Río Cangrejal, Pico Bonito National Park, Honduras.

	Method					
	Ground		Repeat-tree		Single-tree	
Species	%	Rank	%	Rank	%	Rank
Penelope purpurascens	0.7	12	0.0		0.1	
Patagioenas nigrirostris	3.0	7	0.2		0.6	
Aratinga nana	3.7	6	1.3		3.0	6
Pyrilia haematotis	13.0	3	3.6	8	7.7	2
Piaya cayana	0.0		1.5	15	1.0	
Florisuga mellivora	0.0		0.3		1.5	13
Thalurania colombica	0.0		1.6	14	2.1	9
Trogon violaceus	0.7	12	0.5		0.6	
Pteroglossus torquatus	3.7	6	4.7	5	4.1	4
Ramphastos sulfuratus	10.7	4	4.3	6	3.1	5
Melanerpes pucherani	0.0		2.0	11	1.0	
Ornithion semiflavum	1.0	11	1.9	12	1.9	10
Zimmerius vilissimus	0.7	12	1.3		1.3	14
Megarynchus pitangua	0.0		0.1		1.6	12
Tityra semifasciata	3.7	6	2.9	9	2.1	9
Vireo olivaceus	0.3		6.0	3	2.4	8
Hylophilus decurtatus	26.7	1	6.1	2	7.7	2
Vireolanius pulchellus	2.7	8	1.7	13	0.3	
Cyanocorax morio	1.7	9	2.7	10	1.8	11
Polioptila plumbea	1.7	9	3.8	7	4.3	3
Catharus ustulatus	1.3	10	0.3		0.7	
Dendroica pensylvanica	1.3	10	1.9	12	2.1	9
Piranga rubra	0.3		1.5	15	3.0	6
Chlorophanes spiza	0.0		2.0	11	1.2	
Cyanerpes cyaneus	0.7	12	3.8	7	2.7	7
Cyanerpes lucidus	0.0		1.6	14	0.0	
Caryothraustes poliogaster	4.0	5	5.2	4	0.7	
Psarocolius wagleri	13.3	2	12.0	1	7.9	1
Euphonia hirundinacea	0.3		0.2		1.5	13
Euphonia gouldi	0.7	12	1.2		2.1	9
% of total canopy detections	95.7		76.4		70.1	

Detection Rates

I found important differences between detection rates of individual species as well as between groups of species. Secretive migrant and resident species (Table 2.5) were detected at significantly greater hourly rates by canopy methods than from the ground, but between canopy methods detection rates did not differ (Fig. 2.4). I found no significant difference among any of the methods in the hourly detection rate of canopy hummingbirds (Table 2.5), perhaps because of the overall low detection rate of this group. Ground censuses, however, detected only four of seven core canopy hummingbirds, and none in the canopy stratum. I found that the choice of method significantly affected the hourly detection rates of both species ($F_{2,86} = 31.1$, $P < 0.0001$) and individuals ($F_{2,86} = 21.9$, $P < 0.0001$) in the canopy stratum (Fig. 2.5). Similarly, the choice of method significantly affected the hourly detection rates of core canopy species ($F_{2,86} = 20.4$, $P < 0.0001$) and individual core canopy birds ($F_{2,86} = 9.5$, $P = 0.0002$) when detections in all strata were considered (Fig. 2.5). For core canopy species, detection rates were significantly greater for ground censuses than by either canopy method and by the repeat-tree and single-tree methods did not differ (Fig. 2.5). For core canopy individuals the relationship was more complex, although again the detection rate by ground censuses was greatest (Fig. 2.5).

DISCUSSION

Overview

Because a major goal of this study was to test methods for the study of canopy birds, I chose to focus specifically on methods that are either widely available to forest ecologists or which have been used in past studies of canopy birds. Ground-based point counts remain the primary tool for observing forest birds in all levels of the forest because they are easy to conduct and because they are readily adaptable to different environments or particular questions of

TABLE 2.5 Groups of core canopy species used in comparisons of hourly detection rates by the three census methods.

Groups/species
Secretive or inconspicuous species
Migrants
Myiarchus crinitus
Vireo flavifrons
Vireo philadelphicus
Vireo olivaceus
Dendroica petechia
Dendroica pensylvanica
Dendroica magnolia
Dendroica virens
Dendroica castanea
Mniotilta varia
Setophaga ruticilla
Piranga olivacea
Icterus galbula
Residents
Notharchus macrorhynchos
Tolmomyias sulphurescens
Cotinga amabilis
Chlorophanes spiza
Hummingbirds
Florisuga mellivora
Thalurania colombica
Amazilia tzacatl
Heliothryx barroti
Tilmatura dupontii
Highly detectable, conspicuous species
Piaya cayana
Ramphastos sulphuratus
Attila spadiceus
Cyanocorax morio
Thryothorus maculipectus

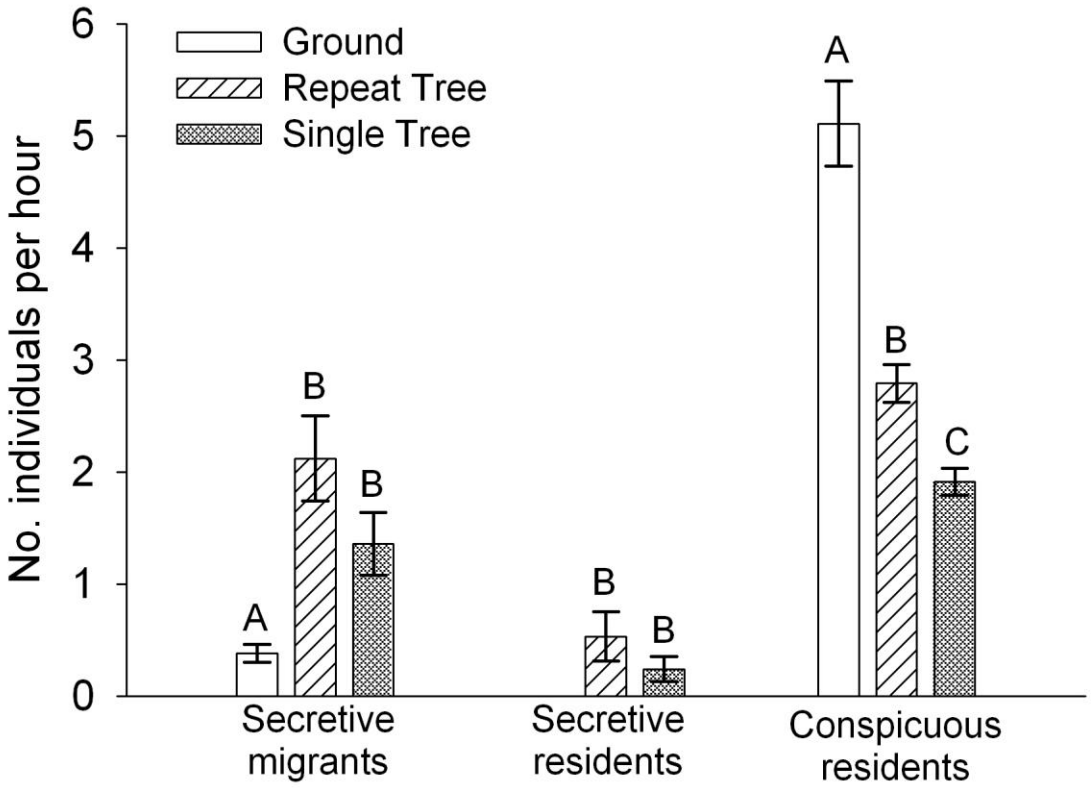


FIGURE 2.4 Hourly detection rates for numbers of individuals of secretive migrant, secretive resident, and conspicuous resident species observed (by sight or sound) by three census methods, Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Means ± 1 SE are shown. Different letters indicate significant differences between groups.

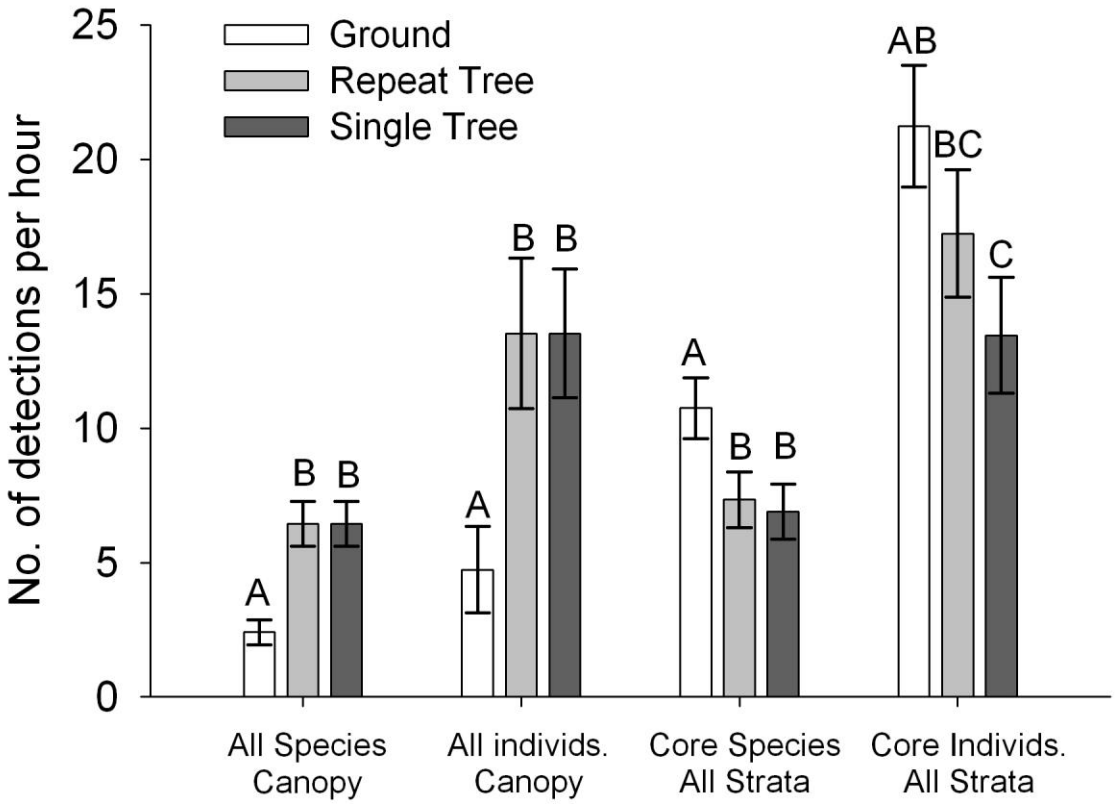


FIGURE 2.5 Hourly detection rates of all species and individuals detected in the canopy stratum and in all forest strata by three census methods in the Río Cangrejal study area, Pico Bonito National Park, Honduras, April 2006–April 2007. Means ± 1 SE are shown. Different letters indicate significant differences between groups.

interest (Ralph et al. 1995). Repeated censuses from one or a small number of canopy viewpoints, as used in pioneering studies of canopy birds (Greenberg 1981, Loiselle 1988, Naka 2004), will continue to be important when canopy access is constrained by the availability of canopy towers or cranes. An important consideration with canopy-based methods is the high temporal and spatial variability of food resources in the canopy (Leigh et al. 1996), which could influence the number of species and individual birds available to the observer. For this reason I incorporated single censuses from trees scattered throughout the study area for comparison with my repeat-tree method. Although a more direct comparison of bird detectability from the canopy and ground could have been obtained by paired canopy and ground observations of equal length, the intended scope of the study was a quantitative comparison of methods. The study design and statistical methods therefore reflect the larger goals of the study.

Detection Probabilities

The spatial distribution, population density, and behavior of a species combined with the choice of method can affect how the proportional abundance of that species at a site is characterized. In this study *Hylophilus decurtatus* was disproportionately predominant in ground censuses and was detected more than twice as often from the ground as from the canopy. This finding is consistent with results from ground-based censuses in central Panama, where Robinson et al. (2000) found *H. decurtatus* to be one of the eight most abundant species. Despite being considered one of the more abundant species at La Selva, Costa Rica (Levey and Stiles 1994), it was not ranked among the most abundant species when canopy-based data alone were used (Loiselle 1988). In contrast, quieter species were systematically overlooked. During ground censuses I failed to detect 67% of all canopy species, including 28% of core canopy species, a result that biased the pattern of familial richness as well.

Two factors, vegetation density and distance between observer and bird, increase dependence on auditory detections (Pacifici et al. 2008). This balance comes with a tradeoff. Increasing vegetation density decreases sound transmittance, and increasing distance between the observer and bird lessens probability of detection (Bibby et al. 2000b, Ellinger and Hödl 2003). In tropical forests, the vocalizations of many species are hard to detect at distances >30 m, and other species call infrequently (Robinson et al. 2000, Blake 2007). These factors increase the dependence on visual detections. Ellinger and Hödl (2003) found that sound waves are scattered by the uneven canopy surface and that species with high-frequency vocalizations compensate by singing above the canopy. In the Río Cangrejal study area the forest averaged 35 to 40 m tall with some trees reaching heights of over 50 m. The combination of forest height and foliage density with the habit of small species with high-frequency voices to sing at the top of the forest undoubtedly decreased the probability of birds in the upper foliage layers being detected. Species underrepresented by ground censuses frequented upper levels of the forest and were disproportionately harder to detect through auditory cues. This result is independent of observer skill, which cannot reduce the amount of obstruction or the distance between a bird at the top of the forest and an observer on the ground. Furthermore, the terrain of the Río Cangrejal study area is uneven and sloping, facilitating viewing into the canopy from the ground. In portions of Amazonia and wherever the terrain is uniformly flat, a ground-based observer is at an even greater disadvantage.

My results also highlight that the probability of detecting birds in the canopy is a function of both census method and bird behavior. Canopy and ground point counts differ in that a canopy point count is conducted at a single point over a long period, whereas a ground transect consists of many distinct point counts of short duration. Remaining at a single station in the

canopy for several hours resulted in rates of detection of birds in the canopy higher than by ground censuses. Species richness by canopy methods was also substantially higher. Ground methods detected conspicuous canopy species more often, partly because during any transect the observer walks through multiple territories of vocal species.

Estimates of Population Density

Robinson et al. (2000) used multiple ground-based methods to estimate population densities for 165 of 252 species in central Panama. Their density estimates for three groups of species were likely affected by the use of ground-based census data. The first group comprised 41 diurnal interior-forest species for which they attempted no estimates because of the birds' high mobility or small sample sizes resulting from difficulty of observation from the ground. Twenty of these species are characteristic of the canopy, including raptors (*Leucopternis albicollis, Falco rufigularis*) and visually conspicuous but otherwise secretive residents (e.g., *Cotinga nattererii*). In contrast, some of these species are readily observed from canopy viewpoints. In Honduras *L. albicollis* may be the single bird most easily observed from the canopy (this study, Anderson 2001); some other raptors are easily observed as well. Canopy-dwelling hummingbirds are notoriously difficult to detect from the ground, yet from my tree vantage points I could often identify and track individual hummingbirds at distances up to 80 m. The second group consisted of some quiet canopy species, (e.g., *Heliothryx barroti, Dendroica pensylvanica, Chlorophanes spiza*), and Robinson et al. (2000) estimated population densities for these. Given that these species are either largely silent or best heard at short distances and are difficult to view from the ground, my results suggest that Robinson et al. (2000) may have underestimated densities of some of them by up to 50%. It is likely that the ground methods of Robinson et al. missed a third group of species altogether, particularly certain Nearctic migrants,

further canopy hummingbirds, and quiet residents. In my study ground censuses revealed 30% fewer species than either canopy method, and the mean estimate of species richness for the study area was approximately 10% lower when the canopy methods were excluded.

Functional Ecology

Understanding the roles of birds in an ecosystem is a central component of tropical forest ecology. For example, much importance has been placed on the role of birds in seed dispersal and in the natural regeneration of forests after disturbance (Cardoso da Silva et al. 1996, Howe 1996, Silva et al. 2002, Cordiero and Howe 2003). Evaluating the potential of the local avifauna to disperse seeds of varying sizes and characteristics requires an accurate depiction of the seed-dispersing guild. My study found that the functional composition of the avifauna was severely misrepresented by census data from the ground only. Among the core canopy birds alone three of seven species of nectarivores, two of four obligate frugivores, and seven of 33 other potential seed dispersers went undetected during ground censuses. For example, *Cotinga amabilis*, a medium-sized frugivore of the forest canopy, was observed frequently during canopy censuses. My observations suggest that, by regurgitating seeds onto tree branches, it plays an important role in seed dispersal of certain Loranthaceae (principally *Psittacanthus rhyncanthus*), hemiparasitic mistletoes that grow on canopy trees. Fruits of these plants are in turn fed on by 19 species of migrant and resident birds, and their flowers are favored by hummingbirds (unpubl. data). Despite the brilliant plumage of the male cotinga, I never detected it from the ground, and all interactions between birds and the Loranthaceae were viewed exclusively from canopy viewpoints. Furthermore, many canopy species detected from the ground through auditory cues were seldom, if ever, observed visually. Understanding the foraging ecology and behavior of canopy species is best accomplished from canopy viewpoints.

Implications for Conservation

Results of this study demonstrate that estimates of population density, species distributions, and local species richness can all be biased by exclusively ground-based methods. I offer two scenarios in which data from ground-based censuses alone could affect conservation practices:

1. Estimates of species richness of birds are often used to determine the conservation importance of particular sites. In sites with identical species richness, differences in forest stature and structure may affect detectability of birds in upper strata and, therefore, bias estimates of richness and the prioritization of conservation potential.

2. Ground-based censuses are often used to describe effects of disturbances, such as selective logging and storm damage, on population densities of birds. Disturbances may affect an observer's ability to detect canopy birds in two ways. First, a disturbance that reduces the amount of foliage in a forest can enhance the observer's ability to see and hear birds at greater heights. Second, a disturbance may affect movement patterns of birds and render them more detectable by the observer. In either case, estimates of population density may be erroneously biased upward. Although forest disturbance may favor some species of birds, changes in detectability may lead to this conclusion when it is actually false.

Canopy-based censuses may be critical for biological monitoring in several respects. Thirty-five species listed as endangered, threatened, or vulnerable by the International Union for the Conservation of Nature (IUCN) inhabit canopies of lowland Neotropical forests (Stotz et al. 1996, BirdLife International 2000). Of these, six are raptors whose population densities are often naturally low and which may be highly visible from canopy viewpoints. Another 13 are frugivores or omnivores that may be important seed dispersers. One is a hummingbird and likely

difficult to detect from the ground. If my results have general applicability, then ground-based surveys will underestimate the densities of these and other inconspicuous species. Additionally, canopy-based censuses may be necessary for monitoring long-term changes in community composition, including species loss following forest fragmentation, as on Barro Colorado Island, Panama, where the difficulty of detecting canopy species may affect estimates of species extirpation and recolonization (Robinson 1999).

RECOMMENDATIONS

Canopy-based methods offer obvious advantages for studies of canopy birds, but the question remains as to what circumstances justify the added effort and expense field work in the canopy requires. Cohn-Haft et al. (1997) demonstrated how canopy surveys from a single canopy tower improve the understanding of an otherwise well-known avifauna. Consequently, long-term data sets at sites of high biological interest, such as tropical field stations, should include canopy methods for a better understanding of trends in canopy bird communities. Rapid ecological assessments may also justify canopy methods, or, if canopy methods are not used, need to state explicitly that ground-based assessments likely miss or underestimate the density of core canopy species.

CHAPTER 3: COMPARATIVE STRUCTURE AND ORGANIZATION OF CANOPY BIRD ASSEMBLAGES IN HONDURAS AND BRAZIL

INTRODUCTION

Bird communities of tropical forests are notoriously diverse, with 250 species co-occurring at single 100-ha sites in Amazonia and over 180 species in southern Middle America (Terborgh et al. 1990, Robinson et al. 2000). Although birds that frequent the forest canopy often constitute 40-50% of the species richness in these communities (Terborgh et al. 1990, Cohn-Haft et al. 1997), the difficulty of accessing the canopy has hindered studies of upper forest levels, such that few published studies have focused directly on canopy bird assemblages and their ecology (Greenberg 1981, Loiselle 1988, Walther 2002, Naka 2004). Despite the limited work on canopy birds, we know that they are an important component of forest bird communities and of the forest ecosystem. Canopy birds include important functional groups such as top predators, seed dispersers, and pollinators (Nadkarni and Matelson 1989, Howe 1996, Blake and Loiselle 2000, Holbrook and Smith 2000, Anderson 2001), and it has been argued that the loss of species in these groups following forest disturbance can have severe consequences for the forest ecosystem (da Silva et al. 1996, Loiselle and Blake 2002, Laurance et al. 2006).

As biodiversity is eroded through the continued impact of humans in lowland Neotropical rainforests, it will be essential to understand the processes that maintain and structure biological communities of forest ecosystems in order to preserve current levels of biodiversity as much as possible. One way to elucidate patterns of diversity and the processes that create and maintain high levels of diversity in the tropics is through a comparative approach looking at similar systems at distant geographic locations (Pitman et al. 2001, Stevens and Willig 2002). Despite the use of this approach to examine bird communities in lowland Neotropical rainforests (Karr et

al. 1990, Robinson et al. 2000), no comparative study has been published that focuses specifically on canopy birds.

Ground-based methods alone are insufficient for the study of canopy birds (Anderson 2009). To date, only three studies have used canopy-based methods to describe bird assemblages in Neotropical forest canopies: two in southern Central America at La Selva, Costa Rica (Loiselle 1988), and Barro Colorado Island, Panama (Greenberg 1981), and one in central Amazonian Brazil (Naka 2004). Although these studies have allowed us a preliminary understanding of canopy bird assemblages, some issues remain unresolved. One key question is whether canopy bird assemblages are dominated by forest birds (Loiselle 1988, Naka 2004) or species associated with open habitats such as edges or clearings (Greenberg 1981). The harsh environment of the two-dimensional forest canopy is similar to open habitats in that it receives more direct sunlight, is subject to dramatic diurnal fluctuations of temperature and humidity and greater seasonal variation in water potential, and experiences greater wind turbulence and evapotransporation than the forest interior (Endler 1993, Koch et al. 2004, Madigosky 2004). As a consequence, we may expect canopy bird assemblages to be dominated by species that tend to occur across open habitat types (Walther 2002, Burney and Brumfield 2009). Second, no consensus has been reached as to the trophic organization of canopy assemblages in lowland Neotropical forests (Greenberg 1981, Loiselle 1988, Naka 2004). Because food resources in the forest canopy are highly variable over space and time (Frankie et al. 1974, Levey et al. 1994, Foster 1996, Leigh 1999), we may expect a high proportion of diet generalists and vagile, migrant species in the canopy that are able to exist on or track a variable and unpredictable diet. Finally, identifying the constituent vertebrate species of any given habitat is a fundamental step in field ecology used to characterize habitats and ecosystems. The characterization of the core constituent species of the lowland Neotropical forest canopy, and differentiating this group from

visitors from other forest strata or neighboring habitats, has remained elusive and has never been quantified.

The major goal of this study was to present a unified description of canopy bird assemblages in lowland Neotropical rainforests. I begin with the first description of a canopy bird assemblage from northern Middle America and use these data as a basis for comparisons with a canopy bird assemblage in central Amazonia similarly censused by means of canopy-based methods. In particular I address the following questions: (1) What differences or similarities exist in the structure and composition of canopy bird assemblages in Honduras and Brazil, in particular species richness, species abundances, composition of dietary guilds, predominance of edge-living species and long-distance migrants at the respective sites? (2) Does species richness of habitat and diet generalists, as well as migrant species in canopy bird assemblages, differ from random expectations drawn from regional species pools? (3) What species may be considered the core constituents of the Neotropical lowland rainforest canopy?

METHODS

Study Areas and Bird Censuses

Analyses are based on fieldwork on canopy birds conducted by me at Pico Bonito National Park in northern Honduras, and data from fieldwork conducted by Naka (2004) in central Amazonia near Manaus, Brazil. Detailed descriptions of the study areas and bird census methods are found in Anderson (2009) and Naka (2004). Briefly, both sites are lowland rainforests found below 350 m elevation. Forest structure is similar, characterized by a closed canopy reaching to approximately 35 m, with abundant epiphytes and lianas. Annual rainfall averages 2900 and 2400 mm for Honduras and Brazil, respectively, and occurs seasonally with a pronounced dry season of approximately 3-5 months.

To make the representative data sets more strictly comparable, there are minor differences in data summarization between the present study and the original ones. I therefore provide a brief overview of census methods before discussing standardization of data. The principle method for studying birds in Honduras and Brazil was censuses from canopy-based viewpoints following the protocol of Loiselle (1988). In Brazil, canopy viewpoints consisted of three canopy towers separated by 10 to 45 km. Three censuses were conducted monthly from each tower over a complete annual cycle from November 1999 to November 2000. In Honduras censuses were conducted from 30 individual trees within a 100-ha plot from April 2006 to April 2007. Additional observations were obtained from 30 point-count stations along two ground transects. Canopy censuses began 30 minutes after sunrise and lasted 3 hours, during which all birds seen or heard in the forest canopy within 150 m of the observer were recorded (Loiselle 1988). The data used in analyses are the maximum number of individuals and species observed per 3-hr canopy census (Loiselle 1988, Naka 2004). For ground point transects in Honduras, numbers of individuals and species were summed for all points covered in a single walking transect. For Honduras only, all birds detected were placed into one of four forest strata: (1) *ground* (soil, leaf litter, and fallen logs); (2) *understory* (the space from the ground to 2 m); (3) *midstory* (the space between the understory and canopy); and (4) *canopy* (the sum of all tree crowns exposed to the sky above; figure 1C in Bongers 2001). I exclude from the present analyses nocturnal species, as well as aerial foragers (swifts, swallows), and scavengers (vultures), because these species were observed solely as flyovers.

To facilitate comparisons at the assemblage level, I assigned all bird species to one of six major feeding guilds: (1) raptors, (2) nectarivores (exclusively hummingbirds), (3) frugivores (diets include a substantial portion of fruit at least during some seasons, seeds not destroyed but presumably dispersed; Moermond and Denslow 1985), (4) granivores (seeds destroyed; herein

parrots), (5) insectivores, and (6) omnivores (species that regularly feed on fruits, insects, nectar, and sometimes small vertebrates). I omit the guild insectivore-omnivore (Naka 2004) and include those species within the omnivore guild. Classification among guilds is based in part on Stiles and Skutch (1989), Terborgh et al. (1990), and Robinson et al. (2000), combined with my own personal observations.

Statistical Analyses

One of my primary objectives was to distinguish the "core" members of the forest canopy. From Remsen (1994) I define the core canopy species as those that regularly breed or winter in, or migrate through, the forest canopy. I exclude from this category those species that are not characteristic of the forest canopy and that occur as visitors from lower levels of the forest, as visitors from non-forest habitats, or as vagrants (Remsen 1994). For Honduras, I used census data to quantify bird preference for the canopy stratum with the method of Neu et al. (1974), which compares the observed frequency of use of a given resource or habitat with an expected frequency derived from the available proportion of that resource or habitat. I established 95% confidence limits, based on Bonferonni's adjustment of the significance level, around the observed frequency of detection in the canopy stratum for species with ≥ 4 detections. A significant preference for the canopy was indicated by expected values below the 95% confidence limits for the observed values (Haney and Solow 1992, da Silva et al. 1996), and species that met this criterion are referred to as the core canopy species. Further, the four vertical strata into which bird observations were placed in Honduras were assigned numeric values (ground = 0, understory = 1, midstory = 2, canopy = 3) so that a stratum average could be calculated for individual species. These procedures could not be applied to Brazil, where detections below the forest canopy were not recorded. Instead, core canopy species were defined qualitatively as those listed by Cohn-Haft et al. (1997) as residents having the forest canopy as

their preferred habitat. Because the method for defining core canopy species differed between Honduras and Brazil, I attempt no quantitative comparisons of core canopy species (e.g., richness, abundance distributions) between sites.

I rarified rates of species accumulation to compare species richness in canopy assemblages. Rarefaction curves are derived from repeated and random resampling of the pool of observations and plotting the average number of species represented by *n* individuals; they are therefore a statistical representation of species-accumulation curves (Gotelli and Colwell 2001, Magurran 2004c). I calculated Chao 1 and Chao 2 nonparametric estimators (Magurran 2004c) to estimate species richness from each study area. These analyses were conducted with EstimateS version 7.5 (Colwell 2005).

I used the Simpson Index (*d*) to characterize dominance of species in Honduras and Brazil (Smith and Wilson 1996, Magurran 2004c). This index was first calculated separately for the overall Honduras and Brazil data sets as an approximation of dominance for the respective canopy bird assemblages. I then used a randomization procedure to obtain confidence limits around the overall values. Specifically, I bootstrapped individual daily censuses until a sample was obtained that contained the same number of censuses as constituted the original empirical sample. This process was iterated 1,000 times to yield 95% confidence limits around the dominance values for the respective canopy assemblages. Bootstrapping and randomization procedures were conducted in R (R Development Core Team 2008).

I used a new approach to determine the 20 dominant canopy species in Honduras and Brazil, a recurrent theme when describing avian communities (Loiselle 1988, Karr et al. 1990, Robinson et al. 2000, Naka 2004). Ideally, dominance is described in terms of the relative density of individuals and biomass (Terborgh et al. 1990, Robinson et al. 2000, MacKenzie et al. 2006), although various proxies have been used in the absence of these data, including

percentage of overall detections (Blake 2007), total number of detections (Loiselle 1988), mean number of individuals detected per census (Naka 2004), and frequency of detection (Naka 2004). To standardize comparisons between sites, I used a procedure that takes into account two such measures of relative abundance: frequency of observation and average number of individuals per observation. Specifically, I multiplied the mean number of individuals per survey and the proportion of surveys in which a species was detected, and ranked species by the product thus obtained. This measure more accurately accounts for the difference between species that are regularly observed in small numbers and species infrequently observed but in larger numbers, usually in single-species flocks.

I compared the observed composition of dietary guilds, numbers of edge species, and numbers of migrant species in the respective core canopy species groups with null distributions drawn from regional species pools through a randomization procedure. At each site I conservatively defined edge species as those found both in continuous forests and forest edges, gardens, or semi-open and non-forest habitats. These determinations were made based primarily on personal experience and published sources (Stotz et al. 1996). To assemble regional species pools I considered all species of possible occurrence in the canopy of primary forest; terrestrial, aquatic, and aerial species were excluded, as were regional species not known to frequent primary forests. For Honduras I considered those species found below 350 m in Pico Bonito National Park (Bonta and Anderson 2002), and for Brazil species listed in Cohn-Haft et al. (1997) as occurring in the Biological Dynamics of Forest Fragments Project (BDFFP) north of Manaus. I used a bootstrapping procedure to randomly draw a number of species from a given regional pool equal to the number of species in the respective core canopy species group. I then tallied the number of edge species, migrants, and species in each dietary guild and repeated this procedure 1,000 times to obtain confidence estimates around a randomly generated assemblage

composition. A result was deemed significant when the observed values fell above or below 95% of the expected values.

For some analyses I desired a balanced comparison of equal survey effort for canopy censuses in Brazil (117 canopy censuses) and Honduras (56 canopy censuses). For this purpose I rarified the Brazil data set to 56 censuses by selecting those censuses that most closely matched the annual Julian dates of the corresponding canopy censuses in Honduras. Analyses that used this restricted data set are noted in the text.

Density Estimation

Previous studies have shown that the great variety of social systems of tropical birds necessitates the use of a variety of methods to estimate population densities, that correcting for observation biases in avian communities with such high species richness is complex and not possible for all species present, and that relationships between true population density of a species and estimates derived from such methods remain unclear (Terborgh et al. 1990, Robinson et al. 2000). The present study investigates distinct avifaunas of distant sites, a fact I acknowledge will introduce bias on density estimation. I emphasize that an attempt at density corrections for a limited number of species under these circumstances would not fully rectify the problem of detection biases in the assemblages under consideration, nor would it allow us to fully address the structure of whole avian assemblages as proposed. Finally, a primary focus of the study was a comparison with the results of the two remaining, canopy-based studies on canopy bird assemblages from Panama (Greenberg 1981) and Costa Rica (Loiselle 1988) for which no corrections would be possible. I instead adhere to the use of detections as a proxy for population density (Greenberg 1981, Loiselle 1988, Karr et al. 1990, Robinson et al. 2000, Naka 2004, Blake 2007), and I restrict comparisons of the data to broad analyses of general patterns that I believe reflect taxonomic and functional patterns of real assemblages and broad-scale

biogeographic patterns that are the result of structuring mechanisms operating at the assemblage level.

RESULTS

Numbers of Detections and Species

From April 2006 to April 2007 I conducted 83 censuses in Honduras (56 canopy censuses and 27 ground transects), resulting in 2538 detections of 118 species in the canopy (Table 3.1). In Brazil, Naka (2004) conducted 117 censuses from November 1999 to November 2000, resulting in 9194 detections of 145 species observed in the canopy (Table 3.1). The combined data set of >11,000 detections is the largest I am aware of for canopy birds.

The rarefaction curve for all canopy species in Brazil is asymptotic, indicating that additional sampling would be unlikely to add more species (Fig. 3.1a). The all-canopy species curve for Honduras has the same shape as the left side of the Brazil curve, but is truncated before reaching the gradual tail of the asymptote (Fig. 3.1a), indicating that sampling was also reasonably complete. More importantly, the curves for core canopy species in both Honduras and Brazil reached asymptotes, signaling that sampling of this group was complete and that few core species remained to be added.

Species richness of canopy bird assemblages appeared similar between Honduras and Brazil. The rarefaction curve for Honduras fell within the 95% confidence interval for the Brazil curve, indicating that richness did not differ significantly between sites (Fig. 3.1a). Expected species richness for Honduras was approximately 130 species, or 20 species fewer than the 150 species expected for Brazil (Fig. 3.1b), although the difference was not statistically significant, based on the level of sampling obtained. Observed species richness in Costa Rica (Loiselle 1988) and Panama (Greenberg 1981) was 86 and 84 species, respectively (Fig. 3.1b).

TABLE 3.1. Number of species and detections (by sight or sound) from the canopy stratum at Pico Bonito National Park, Honduras, and Manaus, Brazil.

			Number of species/number of detections	
Method	Censuses	Census hours	All canopy species	Core canopy species
HONDURAS				
Ground	27	66.7 (2.4±0.56)	36/300	31/294
Repeat-tree	28	84 (3±0)	100/1239	65/1191
Single-tree	28	84 (3±0)	103/999	66/923
All trees	56	168 (3±0)	118/2238	66/2114
Total	83	234.7	118/2538	66/2408
BRAZIL				
Towers (all surveys)	117	351 (3±0)	145/9194	107/8814
Towers (rarified)	56	168 (3±0)	138/4575	107/4360

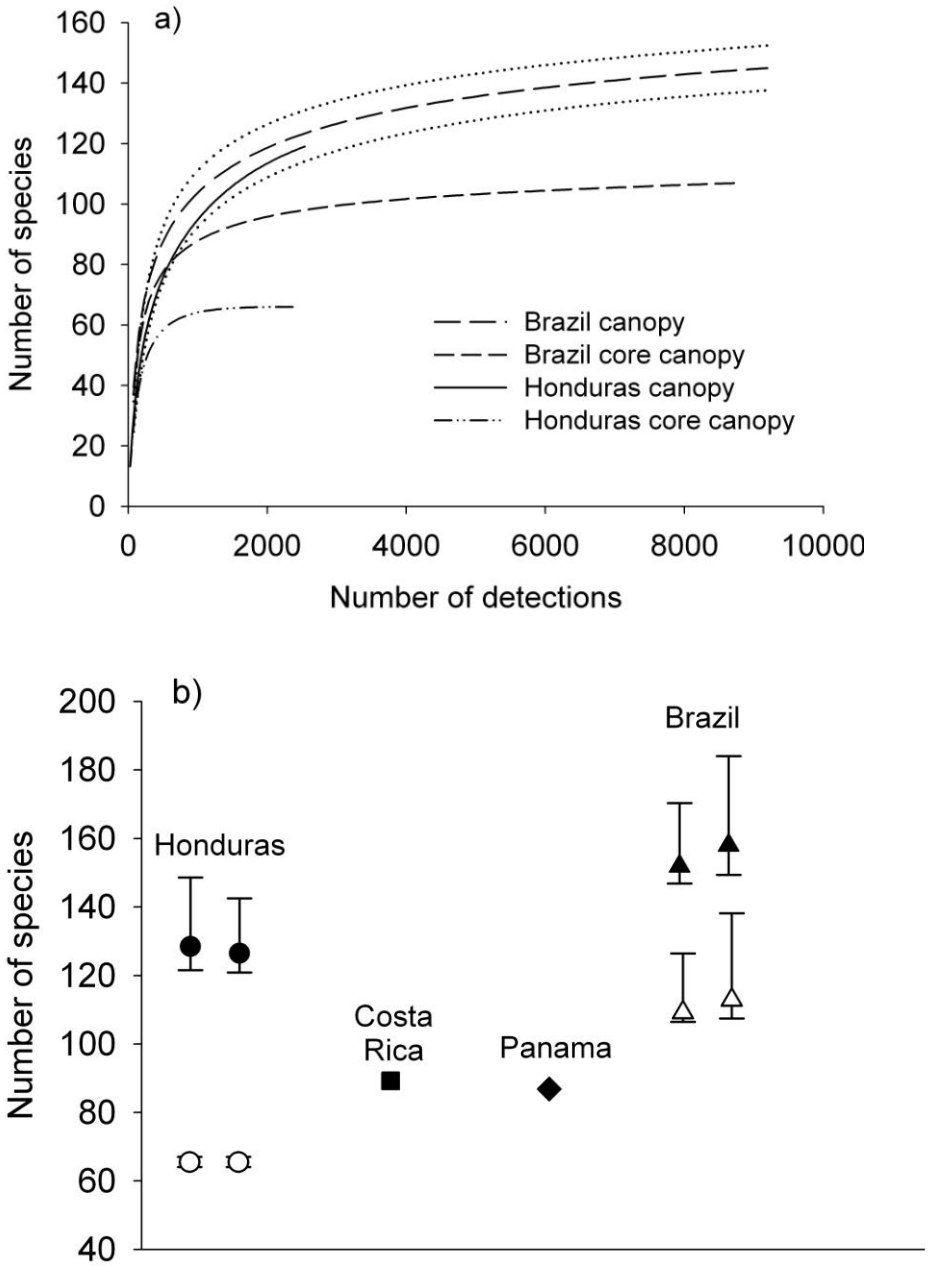


FIGURE 3.1. Individual-based rarefaction curves (a) and corresponding estimates of species richness (b) for canopy bird assemblages in Honduras and Brazil. Dotted line around Brazil canopy curve depicts 95% confidence interval. b) Pairs of richness estimates correspond to Chao 1 and Chao 2 estimators, respectively. Shapes and bars represent means and 95% confidence intervals respectively. Solid shapes represent all species observed in the canopy, and hollow shapes represent core canopy species only. Numbers of species observed in Costa Rica (Loiselle 1988) and Panama (Greenberg 1981) canopies are also shown.

Core Canopy Species

The core canopy species in Honduras were represented by 66 species, or 60% of all species observed in the canopy (Table 3.2). Twenty of these were observed exclusively in the canopy stratum, as represented by a stratum mean of 3.0 (Table 3.2). An additional 25 species were observed disproportionately more often in the canopy, as indicated by a stratum average of 2.9 or higher. Together these 45 species can be classified as canopy specialists. In Brazil, 107 species (74% of all species detected in the canopy) were considered core canopy species. A total of 49 genera encompassing 155 species were reported from the canopy at a minimum of three sites amongst Honduras, Costa Rica, Panama, and Brazil. Twenty-six genera historically occurred at all sites (*Ara* and *Amazona* having been extirpated from some), and three species (*Florisuga mellivora*, *Chlorophanes spiza*, *Cyanerpes cyaneus*) were observed at all sites (Table 3.3). Together this group can be taken as the core representatives that characterize canopy bird assemblages of these lowland Neotropical rainforests. The family Tyrannidae showed the greatest richness, with 13 genera and 35 species represented. The most species-rich genera were *Euphonia* with eight species represented, and *Trogon*, *Dendroica*, and *Tangara*, each with seven species. Migrants were well represented, with high richness in the genera *Dendroica* and *Vireo* (four species).

Species Abundances

The distribution of species' abundances in Honduras was significantly different from that in Brazil when sampling was restricted to 56 canopy censuses for each site (Kolmogorov-Smirnov test, $P<0.001$). Three lines of evidence indicate that abundance distributions were more even for Brazil than Honduras. First, three important differences in rank-abundance curves are noteworthy: 1) Honduras has a greater importance of super-abundant species; 2) the middle portion of the Brazil curve lies completely above the Honduras curve; and 3) the tail of rare

TABLE 3.2. All bird species observed on the 100-ha study site at Pico Bonito National Park, Honduras, April 2006 to April 2007. Species observed in the canopy and those designated as core canopy species are noted, as well as species observed outside of standardized survey times.

					No. of canopy detections/ no. surveys detected in canopy		
Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. det. (%)	Mean no. individs.	No. surveys (%)
Tinamidae							
Tinamus major	R	study	F				
Crypturellus boucardi	R	study	O				
Cracidae							
Ortalis vetula	R	study	O				
Penelope purpurascens	R	canopy	F	-	3 (0.1)	0.0	2 (2.4)
Crax rubra	R	study	F				
Odontophoridae							
Rhynchortyx cinctus	R	study	G				
Cathartidae							
Coragyps atratus	R	aerial, out	S				
Cathartes aura	R	aerial	S				
Accipitridae							
Harpagus bidentatus	R	aerial	RD				
Leucopternis albicollis	R	**core**	RD	3±0.0	13 (0.5)	0.2	10 (12)
Buteogallus urubitinga	R	canopy	RD	-	3 (0.1)	0.0	3 (3.6)
Spizaetus tyrannus	R	aerial	RD				
Spizaetus ornatus	R	aerial	RD				
Falconidae							
Micrastur semitorquatus	R	study	RD				
Falco rufigularis	R	canopy, out	RD				
Columbidae							
Patagioenas flavirostris	R	canopy	F	-	1 (0)	0.0	1 (1.2)

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Patagioenas nigrirostris	R	**core**	F	2.9±0.3	16 (0.6)	0.2	12 (14.5)
Claravis pretiosa	R	canopy	F	-	2 (0.1)	0.0	1 (1.2)
Leptotila cassini	R	study	F				
Geotrygon albifacies	EM	study	F				
Geotrygon montana	R	study	F				
Psittacidae							
Aratinga nana	R	**core**	G	3±0.2	53 (2.1)	0.6	17 (20.5)
Pyrilia haematotis	R	**core**	G	3±0.1	191 (7.5)	2.3	38 (45.8)
Pionus senilis	R	canopy	G	-	2 (0.1)	0.0	1 (1.2)
Cuculidae							
Piaya cayana	R	**core**	I	2.7±0.5	30 (1.2)	0.4	27 (32.5)
Coccyzus americanus	NMT	canopy	I	-	3 (0.1)	0.0	2 (3.7)
Coccyzus minor	R	study	I				
Strigidae							
Lophostrix cristata	R	noct	RN				
Glaudicium griseiceps	R	noct	RN				
Ciccaba virgata	R	noct	RN				
Caprimulgidae							
Nyctidromus albicollis	R	noct	I				
Caprimulgus vociferus	NMR	noct	I				
Nyctibiidae							
Nyctibius grandis	R	noct	I				
Apodidae							
Streptoprocne zonaris	R	aerial	I				
Chaetura pelagica	NMT	aerial	I				
Chaetura vauxi	NMR	aerial	I				
Panyptila cayennensis	R	aerial	I				

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Trochilidae							
Phaethornis longirostris	R	canopy	N	-	1 (0)	0.0	1 (1.2)
Phaethornis striigularis	R	study	N				
Campylopterus hemileucurus	R	canopy	N		1 (0)	0.0	1 (1.2)
Florisuga mellivora	R	**core**	N	3±0.1	20 (0.8)	0.2	14 (16.9)
Colibri delphinae	R	canopy	N	-	1 (0)	0.0	1 (1.2)
Anthracothorax prevostii	R	canopy	N	-	1 (0)	0.0	1 (1.2)
Klais gumeti	R	canopy	N	-	1 (0.2)	0.0	1 (1.2)
Lophornis helenae	R	**core**	N	3±0.0	4 (0.2)	0.1	3 (3.6)
Thalurania colombica	R	**core**	N	2.8±0.4	35 (1.4)	0.4	29 (34.9)
Hylocharis eliciae	R	**core**	N	3±0.2	11 (0.4)	0.1	8 (9.6)
Amazilia candida	R	**core**	N	2.9±0.3	22 (0.9)	0.3	19 (22.9)
Amazilia cyanocephala	R	canopy	N	-	1 (0)	0.0	1 (1.2)
Amazilia tzacatl	R	**core**	N	3±0.0	7 (0.3)	0.1	7 (8.4)
Eupherusa eximia	EM	study	N				
Heliothryx barroti	R	core	N	2.6±0.9	4 (0.2)	0.1	4 (4.8)
Tilmatura dupontii	EM	**core**	N	3±0.0	5 (0.2)	0.1	5 (6)
Trogonidae							
Trogon massena	R	**core**	O	2.7±0.5	9 (0.4)	0.1	8 (9.6)
Trogon violaceus	R	**core**	O	2.6±0.5	16 (0.6)	0.2	15 (18.1)
Trogon rufus	R	canopy	O	-	2 (0)	0.0	2 (2.4)
Trogon collaris	R	canopy	O	2.4±0.5	7 (0.1)	0.1	5 (6)
Momotidae							
Hylomanes momotula	R	study	I				
Momotus momota	R	study	O				
Electron carinatum	R	canopy	O	-	3 (0.1)	0.0	3 (3.6)

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Bucconidae							
Notharchus hyperrhynchus	R	**core**	I	3±0.0	7 (0.3)	0.1	3 (3.6)
Galbulidae							
Galbula ruficauda	R	canopy	I	2.6±0.5	4 (0.2)	0.1	4 (4.8)
Ramphastidae							
Aulacorhynchus prasinus	R	**core**	F	3±0.0	5 (0.2)	0.1	3 (3.6)
Pteroglossus torquatus	R	**core**	F	2.9±0.3	102 (40)	1.2	30 (36.1)
Selenidera spectabilis	R	canopy	F	-	3 (0.1)	0.0	3 (3.6)
Ramphastos sulfuratus	R	**core**	F	3±0.2	127 (5)	1.5	54 (65.1)
Picidae							
Picumnus olivaceus	R	canopy	I	-	1 (0)	0.0	1 (1.2)
Melanerpes pucherani	R	**core**	O	2.9±0.3	39 (1.5)	0.5	27 (32.5)
Picoides fumigatus	R	**core**	I	2.7±0.5	13 (0.5)	0.2	12 (14.5)
Celeus castaneus	R	**core**	O	2.8±0.4	5 (0.2)	0.1	4 (4.8)
Campephilus guatemalensis	R	canopy	I	-	1 (0)	0.0	1 (1.2)
Furnariidae							
Xenops minutus	R	canopy	I	2.7±0.5	4 (0.2)	0.1	4 (4.8)
Sclerurus guatemalensis	R	study	I				
Glyphorhynchus spirurus	R	canopy	I	-	2 (0.1)	0.0	2 (2.4)
Dendrocincla anabatina	R	study	I				
Dendrocincla homochroa	R	study	I				
Xiphocolaptes promeropirhynchus	R	canopy	I	-	2 (0.1)	0.0	2 (2.4)
Dendrocolaptes sanctihomae	R	canopy	I	-	3 (0.1)	0.0	2 (2.4)
Xiphorhynchus susurrans	R	canopy	I	-	2 (0.1)	0.0	2 (2.4)

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Xiphorhynchus flavigaster	R	**core**	I	2.6±0.6	8 (0.3)	0.1	8 (9.6)
Lepidocolaptes souleyetii	R	study	I				
Thamnophilidae							
Thamnophilus atrinucha	R	canopy	I	-	3 (0.1)	0.0	3 (3.6)
Thamnistes anabatinus	R	canopy	I	-	3 (0.1)	0.0	2 (2.4)
Microrhopias quixensis	R	canopy	I	2.2±0.6	7 (0.3)	0.1	3 (3.6)
Cercromacra tyrannina	EM	study	I				
Gymnopithys leucaspis	R	study	I				
Formicariidae							
Formicarius analis	R	study	I	-			
Tyrannidae							
Ornithion semiflavum	R	**core**	O	3±0.0	41 (1.6)	0.5	36 (43.4)
Myiopagis viridicata	R	canopy	I	-	3 (0.1)	0.0	3 (3.6)
Mionectes oleagineus	R	**core**	O	2.6±0.6	13 (0.5)	0.2	12 (14.5)
Leptopogon amaurocephalus	R	canopy	I	2.6±0.5	4 (0.2)	0.1	3 (3.6)
Zimmerius vilissimus	R	**core**	O	3±0.0	26 (1)	0.3	20 (24.1)
Oncostoma cinereigulare	R	study	I				
Rhynchocyclus brevirostris	R	study	I				
Tolmomyias sulphurescens	R	**core**	O	3±0.0	7 (0.3)	0.1	7 (8.4)
Platyrinchus cancrominus	R	study	I	-			
Onychorhynchus coronatus	R	study	I	-			
Terenotriccus erythrurus	R	canopy	I	-	2 (0.1)	0.0	2 (2.4)
Myiobius sulphureipygius	R	study	I	-			
Contopus cooperi	NMT	canopy	I	-	1 (0)	0.0	1 (1.5)
Contopus spp.[e]	NMR	**core**	I	2.7±0.6	17 (0.7)	0.2	14 (20.9)
Contopus sordidulus	NMR	study	I	-		-	
Contopus virens	NMT	study	I	-		-	

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Empidonax spp.[f]	NMR	**core**	I	2.8±0.4	15 (0.6)	0.2	14 (34.1)
Empidonax virescens	NMT	study	I	-		-	
Empidonax trailii	NMR	study	I	-		-	
Attila spadiceus	R	**core**	O	2.9±0.3	23 (0.9)	0.3	21 (25.3)
Rhytipterna holyerythra	R	canopy	O	-	3 (0.1)	0.0	3 (3.6)
Myiarchus tuberculifer	R	**core**	I	3±0.0	18 (0.7)	0.2	13 (15.7)
Myiarchus crinitus	NMR	**core**	I	3±0.0	4 (0.2)	0.1	3 (4.3)
Myiarchus tyrannulus	R	canopy	I	-	1 (0)	0.0	1 (1.2)
Megarynchus pitangua	R	**core**	O	3±0.0	16 (0.6)	0.2	7 (8.4)
Myiozetetes similis	R	canopy	O	-	3 (0.1)	0.0	2 (2.4)
Myiodynastes luteiventris	AM	**core**	O	2.7±0.5	9 (0.4)	0.1	6 (16.7)
Schiffornis turdina	R	canopy	O	-	2 (0.1)	0.0	2 (2.4)
Pachyramphus major	R	canopy, out	I				
Pachyramphus aglaiae	R	canopy	I	-	3 (0.1)	0.0	2 (2.4)
Tityra semifasciata	R	**core**	O	3±0.0	64 (2.5)	0.8	27 (32.5)
Tityra inquisitor	R	canopy	O	-	2 (0.1)	0.0	1 (1.2)
Cotingidae							
Cotinga amabilis	R	**core**	F	3±0.0	21 (0.8)	0.3	14 (16.9)
Pipridae							
Manacus candei	R	canopy	F	-	3 (0.1)	0.0	2 (2.4)
Pipra mentalis	R	canopy	F	-	1 (0)	0.0	1 (1.2)
Vireonidae							
Vireo flavifrons	NMR	**core**	I	3±0.0	14 (0.6)	0.2	13 (17.8)
Vireo gilvus	NMR	canopy	I	-	3 (0.1)	0.0	2 (2.7)
Vireo philadelphicus	NMR	**core**	I	3±0.0	8 (0.3)	0.1	5 (6.8)
Vireo olivaceus	NMT	**core**	O	2.9±0.3	112 (4.4)	1.4	31 (57.4)

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Hylophilus ochraceiceps	R	canopy	I	2.3±0.4	7 (0.3)	0.1	3 (3.6)
Hylophilus decurtatus	R	**core**	O	3±0.1	226 (8.9)	2.7	75 (90.4)
Vireolanius pulchellus	R	**core**	O	3±0.0	32 (1.3)	0.4	18 (21.7)
Corvidae							
Cyanocorax morio	R	**core**	O	2.9±0.4	54 (2.1)	0.7	28 (33.7)
Hirundinidae							
Stelgidopteryx serripennis	R	aerial	I				
Troglodytidae							
Thryothorus maculipectus	R	**core**	I	2.4±0.6	23 (0.9)	0.3	15 (18.1)
Henicorhina leucosticta	R	study	I				
Microcerculus philomena	R	study	I				
Polioptilidae							
Ramphocaenus melanurus	R	canopy	I	2.1±0.5	8 (0.3)	0.1	8 (9.6)
Polioptila plumbea	R	**core**	I	3±0.1	85 (3.3)	1.0	49 (59)
Turdidae							
Myadestes unicolor	R	study	O				
Catharus ustulatus	NMR	**core**	O	2.7±0.7	16 (0.6)	0.2	11 (15.1)
Hylocichla mustelina	NMR	canopy	O	-	1 (0)	0.0	1 (1.4)
Turdus grayi	V	canopy	O	-	1 (0)		1 (1.2)
Turdus assimilis	EM	canopy	O	-	1 (0)	0.0	1 (1.2)
Parulidae							
Vermivora peregrina	NMR	**core**	O	2.9±0.3	14 (0.6)	0.2	8 (11.1)
Dendroica petechia	NMR	**core**	I	3±0.0	6 (0.2)	0.1	6 (7.5)
Dendroica pensylvanica	NMR	**core**	O	3±0.1	42 (1.7)	0.5	34 (46.6)
Dendroica magnolia	NMR	**core**	I	2.9±0.3	20 (0.8)	0.2	19 (26)
Dendroica virens	NMR	**core**	I	3±0.0	13 (0.5)	0.2	12 (16.4)
Dendroica fusca	NMT	canopy	O	-	3 (0.1)	0.0	3 (5.6)

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Dendroica castanea	NMT	**core**	O	2.9±0.2	10 (0.4)	0.1	6 (8.7)
Dendroica cerulea	NMT	canopy, out	I				
Mniotilta varia	NMR	**core**	I	2.8±0.4	13 (0.5)	0.2	12 (29.3)
Setophaga ruticilla	NMR	**core**	I	2.9±0.3	13 (0.5)	0.2	13 (16.3)
Helmitheros vermivorum	NMR	canopy	I	-	2 (0.1)	0.0	2 (2.7)
Seiurus noveboracencis	NMR	study	I				
Seiurus aurocapilus	NMR	study	I				
Seiurus motacilla	NMR	study	I				
Oporornis formosus	NMR	study	I				
Wilsonia citrina	NMR	study	I				
Wilsonia pusilla	NMR	canopy	I	-	1 (0)	0.0	1 (1.4)
Wilsonia canadensis	NMT	canopy, out	I				
Myioborus miniatus	EM	canopy	I	-	1 (0)	0.0	1 (1.2)
Basileuterus culicivorus	R	study	I				
Basileuterus fulvicauda	R	study	I				
Thraupidae							
Lanio aurantius	R	**core**	O	3±0.0	9 (0.4)	0.1	7 (8.4)
Chlorophanes spiza	R	**core**	O	3±0.0	28 (1.1)	0.3	10 (12)
Cyanerpes lucidus	R	**core**	O	3±0.0	15 (0.6)	0.2	2 (2.4)
Cyanerpes cyaneus	R	**core**	O	3±0.1	101 (4)	1.2	29 (34.9)
Cardinalidae							
Piranga rubra	NMR	**core**	O	3±0.1	37 (1.5)	0.5	26 (35.6)
Piranga olivacea	NMT	**core**	O	2.9±0.2	25 (1)	0.0	12 (28.6)
Piranga leucoptera	R	canopy	O	-	2 (0.1)	0.0	2 (2.4)
Habia rubica	R	study	O				

TABLE 3.2 continued

Family and species	Residency Status[a]	Canopy Status[b]	Feeding Guild[c]	Stratum Mean±SD[d]	No. of canopy detections/ no. surveys detected in canopy: No. det. (%)	Mean no. individs.	No. surveys (%)
Habia fuscicauda	R	study	O				
Thraupis abbas	R	canopy	O	-	3 (0.1)	0.0	2 (2.4)
Saltator coerulescens	R	study	O				
Caryothraustes poliogaster	R	**core**	O	2.8±0.4	66 (2.6)	0.8	6 (7.2)
Pheucticus ludovicianus	NMR	canopy	O	-	2 (0.1)	0.0	2 (3.1)
Cyanocompsa cyanoides	R	study	O	-			
Icteridae							
Quiscalus mexicanus	V	canopy	O	-	1 (0)		1 (1.2)
Icterus galbula	NMR	**core**	O	3±0.0	19 (0.7)	0.2	14 (18.2)
Psarocolius wagleri	R	**core**	O	3±0.2	321 (12.6)	3.9	33 (39.8)
Psarocolius montezuma	R	**core**	O	3±0.0	13 (0.5)	0.2	9 (10.8)
Fringillidae							
Euphonia affinis	R	canopy	O	-	1 (0)	0.0	1 (1.2)
Euphonia hirundinacea	R	**core**	O	2.9±0.3	19 (0.7)	0.2	10 (12)
Euphonia gouldi	R	**core**	O	2.7±0.5	31 (1.2)	0.4	22 (26.5)
Euphonia minuta	R	**core**	I	3±0.0	7 (0.3)	0.1	4 (4.8)

[a]AM, austral migrant; EM, elevational migrant; NMR, Neartic migrant resident; NMT, Nearctic resident transient; R, resident; V, vagrant.

[b]aerial, species observed solely as flyovers; canopy, species observed in the canopy; core, species considered part of the core canopy assemblage; out, species observed outside the boundaries of the plot or not during standardized surveys; noct, nocturnal species; study, species observed on the 100-ha plot but not in the canopy.

[c]F, frugivore; G, granivore; I, insectivore; N, nectarivore; RD, diurnal raptor; RN, nocturnal raptor; S, scavenger.

[d]Stratum means are given only for species represented by ≥4 individuals observed in the canopy.

[e]Individuals of *Contopus sordidulus* and *C. virens* could not be reliably identified to species and were treated as a single species for analyses.

[f]Individuals of *Empidonax virescens* and *E. trailii* could not be reliably identified to species and were treated as a single species for analyses.

TABLE 3.3. Core canopy species of lowland Neotropical rainforests as represented by genera observed in the canopy of four lowland Neotropical rainforests with published canopy studies: Pico Bonito National Park, Honduras (Anderson 2009), La Selva, Costa Rica (Loiselle 1988), Barro Colorado Island, Panama (Greenberg 1981), and Manaus, Brazil (Naka 2004). Only genera observed at ≥ 3 sites are included. Genera considered part of the core canopy assemblages at the Honduras (Ho) or Brazil sites (Br) are noted.

Genus	Core Species	No. Species	No. Sites
Leucopternis	Ho, Br	3	3
Patagioenas	Ho, Br	4	3
Amazona[a]	Br	2	3
Ara[a]	Br	2	1
Brotogeris	Br	2	3
Pionus	Br	3	4
Piaya	Ho, Br	2	4
Florisuga	Ho, Br	1	4
Heliothryx	Ho	2	4
Thalurania	Ho, Br	2	3
Trogon	Ho, Br	7	4
Notharchus	Ho, Br	3	4
Pteroglossus	Ho, Br	2	4
Ramphastos	Ho, Br	4	4
Selenidera	Ho, Br	2	3
Campephilus	Ho	3	4
Celeus	Ho, Br	4	3
Melanerpes	Ho	2	4
Xiphorhynchus	Ho	5	3
Attila[b]	Ho, Br	1	2
Contopus	Ho	3	3
Mionectes	Ho	3	3
Myiarchus	Ho	4	4
Myiodynastes	Ho	2	3
Myiopagis	Br	3	3
Myiozetetes	--	2	3
Ornithion	Ho, Br	3	3
Pachyramphus	Br	5	3
Rhytipterna	Br	2	3
Tityra	Ho, Br	3	4
Tolmomyias	Ho, Br	3	4
Zimmerius	Ho, Br	2	4
Cotinga	Ho, Br	4	3
Hylophilus	Ho, Br	3	4
Vireo	Ho, Br	5	3
Vireolanius	Ho, Br	2	3
Polioptila	Ho, Br	2	4
Dendroica	Ho	7	4
Vermivora	Ho	1	3
Chlorophanes	Ho, Br	1	4

TABLE 3.3 continued

Genus	Core Species	No. Species	No. Sites
Cyanerpes	Ho, Br	4	4
Dacnis	Br	3	4
Tachyphonus	Br	4	3
Tangara	Br	7	3
Caryothraustes	Ho, Br	2	3
Piranga	Ho	3	3
Thraupis	Br	3	3
Icterus	Ho, Br	2	4
Psarocolius	Ho, Br	3	4
Euphonia	Ho, Br	8	4

[a]*Ara* and *Amazona* historically occurred at all sites, but have been extirpated from some.
[b]*Attila spadiceus* is included because it was considered a core species for both Honduras and Brazil and occurred in high densities at both sites.

species is longer for Brazil (Fig. 3.2). Second, the 20 most abundant species make up a greater proportion of the canopy assemblage in Honduras than in Brazil (Table 3.4). In Honduras, the top 20 species accounted for 68.9% of all canopy detections, and seven species (*Hylophilus decurtatus*, *Psarocolius wagleri*, *Pyrilia haematotis*, *Ramphastos sulfuratus*, *Vireo olivaceus*, *Pteroglossus torquatus*, *Cyanerpes cyaneus*) each accounted for ≥4% of total detections. In Brazil the 20 most abundant species accounted for 48.5% of total detections, and only one species (*Brotogeris chrysopterus*) accounted for ≥ 4% of total detections. Third, results from bootstrapping analyses of diversity indices revealed greater evenness in the Brazil canopy assemblage and greater dominance for Honduras (Table 3.5).

Trophic Organization

The two dominant foraging guilds in Honduras in terms of species richness were omnivores and insectivores, both of which had nearly four times as many species as any other guild (Fig. 3.3). Omnivores, however, dominated in terms of numerical abundance, comprising 49% of total canopy detections, followed by insectivores (23%) and nectarivores (12%). Granivores (10%), frugivores (7%) and diurnal raptors (1%) all accounted for 10% or less of total detections. The pattern for species richness in Brazil was overall similar, with omnivores and insectivores being the most species-rich guilds, although the pattern of relative abundance, when measured in terms of numbers of detections by guild, differed from the pattern found in Honduras. In Brazil, omnivores also had more overall detections (41%), followed by insectivores (23%), granivores (20%), and frugivores (14%). Nectarivores (2%) and diurnal raptors (1%) each constituted fewer than 10% of total canopy detections. Guild composition differed between sites when compared at the level of all species detected in the canopy (Chi-Square $_{(5, 255)}$ 18.80, P=0.0021; Fig. 3.3a), and at the level of core canopy species (Chi-Square $_{(5, 163)}$ 13.88, P=0.0164; Fig. 3.3b). However, when species that had been locally extirpated from

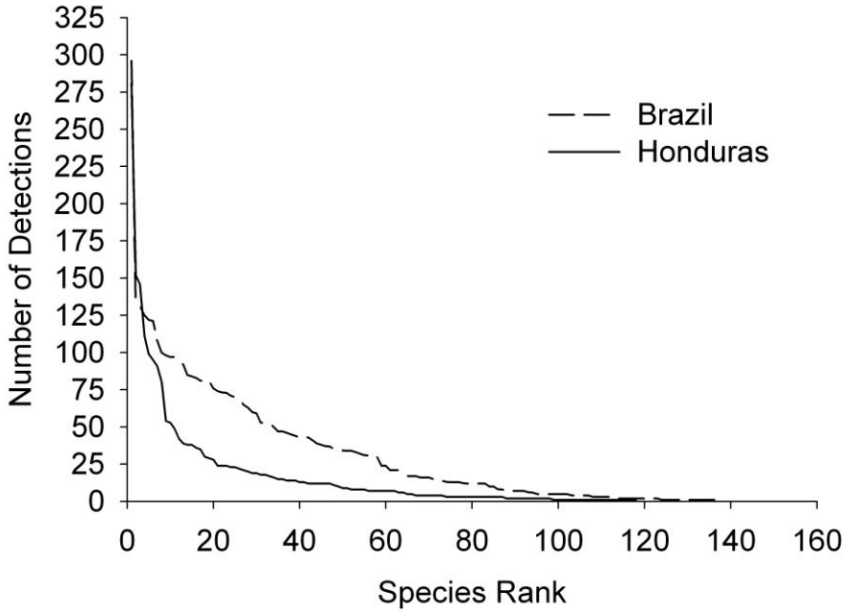


FIGURE 3.2. Rank-abundance curves based on numbers of detections by sight or sound of canopy birds in the Manaus study area, Brazil, November 1999-November 2000, and Pico Bonito National park study area, Honduras, April 2006-April 2007. Data are derived from 56 canopy censuses at each site.

TABLE 3.4. The twenty dominant species recorded from the forest canopy in Pico Bonito National Park, Honduras, and Manaus, Brazil. Dominance rankings are calculated as the product of mean number of detections per census and percent censuses detected (see text). Species are sorted in descending order of relative dominance.

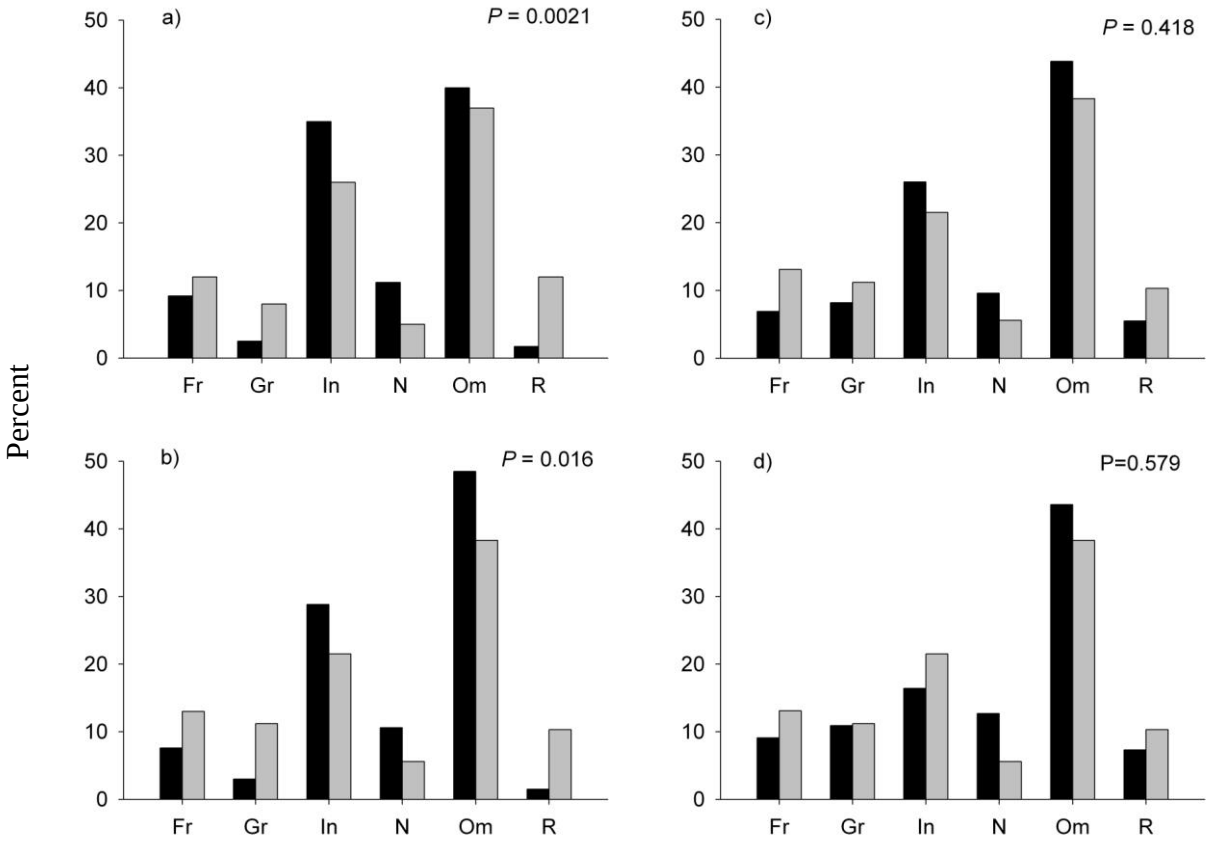
Species	% Total detections	Mean no. detections	% Surveys
Honduras			
Hylophilus decurtatus	8.9	2.7	90.4
Psarocolius wagleri	12.6	3.9	39.8
Pyrilla haematotis	7.5	2.3	45.8
Ramphastos sulfuratus	5.0	1.5	65.1
Vireo olivaceus	4.4	1.4	57.4
Polioptila plumbea	3.3	1.0	59.0
Pteroglossus torquatus	4.0	1.2	36.1
Cyanerpes cyaneus	4.0	1.2	34.9
Tityra semifasciata	2.5	0.8	32.5
Dendroica pensylvanica	1.7	0.5	46.6
Cyanocorax morio	2.1	0.7	33.7
Ornithion semiflavum	1.6	0.5	43.4
Piranga rubra	1.5	0.5	35.6
Melanerpes pucherani	1.5	0.5	32.5
Thalurania colombica	1.4	0.4	34.9
Aratinga nana	2.1	0.6	20.5
Piaya cayana	1.2	0.4	32.5
Euphonia gouldi	1.2	0.4	26.5
Piranga olivacea	1.0	0.3	28.6
Vireolanius pulchellus	1.3	0.4	21.7
Total	68.9		
Brazil			
Brotogeris chrysopterus	7.3	5.7	79.5
Dacnis cayana	2.8	2.2	86.3
Galbula dea	2.5	1.9	93.2
Zimmerius gracilipes	2.2	1.8	97.4
Herpsilochmus dorsimaculatus	2.3	1.8	90.6
Ramphastos tucanus	2.3	1.8	80.3
Vireolanius leucotis	2.0	1.6	92.3
Hylophilus muscicapinus	1.9	1.5	86.3
Terenura spodioptila	1.9	1.5	82.9
Patagioenas plumbea	1.9	1.5	81.2
Tangara punctata	2.1	1.6	74.4
Cyanerpes cyaneus	2.3	1.8	67.5
Tachyphonus cristatus	2.0	1.5	76.9
Tolmomyias assimilis	1.7	1.4	84.6

TABLE 3.4 continued

Species	% Total detections	Mean no. detections	% Surveys
Chlorophanes spiza	1.9	1.5	76.1
Lamprozpiza melanoleuca	2.0	1.6	70.1
Tangara chilensis	2.8	2.2	49.6
Amazona autumnalis	2.6	2.1	47.9
Xipholena punicea	1.7	1.4	70.1
Pionus menstruus	2.4	1.9	48.7
Total	48.5		

TABLE 3.5. Significance tests evaluating differences in diversity indices between Honduras and Brazil canopy bird assemblages. Assemblage values were derived from the entire data set for each assemblage. 95% confidence intervals derived from bootstrapping individual samples are shown.

	Honduras		Brazil	
Index	Assemblage value	95% CI	Assemblage value	95% CI
Simpson D (dominance)	0.04	0.03-0.06	0.02	0.02-0.02



FIGUREE 3.3. Guild composition of canopy bird assemblages in Pico Bonito National Park, Honduras, and Manaus, Brazil. a) all birds observed in the canopy, b) core canopy species only, c) core canopy species including canopy species extirpated from Honduras, d) core canopy species excluding Nearctic migrants. Black bars are for Honduras, gray bars Brazil. Guild abbreviations represent frugivores (Fr), granivores (Gr), insectivores (In), nectarivores (N), omnivores (Om), and raptors (R).

Honduras (*Ara macao*, *Amazona farinosa*, *A. autumnalis*) or whose populations were likely reduced through human persecution (*Buteogallus urubitinga*, *Harpagus bidentatus*, *Falco rufigularis*, *Pionus senilis*) were added to the analysis, the composition of dietary guilds within core canopy species was indistinguishable (Chi-Square $_{(5, 170)}$ 4.99, P=0.418; Fig. 3.3c). This relationship held when Nearctic migrants were excluded (Chi-Square $_{(5, 157)}$ 3.80, P=0.579; Fig. 3.3d), demonstrating that the similarity in guild composition between Honduras and Brazil was not affected by migrant species richness.

Omnivore species were overrepresented in both canopy assemblages when compared with null expectations drawn from regional species pools (Table 3.6). In addition, raptor species were underrepresented in Honduras, whereas granivores were overrepresented and insectivores were underrepresented in Brazil when compared with the null expectation (Table 3.6).

Habitat Affiliations

Edge species were not an important component of either canopy assemblage. In both Honduras and Brazil the number of core canopy species that are characteristic of edges and open habitats was significantly less than the null expectation drawn the regional species pools (Table 3.6).

Migratory Status

The number of long-distance migrants occurring as core canopy species in Honduras did not differ statistically from the null expectation. However, migrants appear to be a relatively important component of the Honduras canopy assemblage, accounting for 19 core canopy species (29% of core canopy species, Table 3.7) and four of the top 20 species (Table 3.4). Long-distance migrants were relatively less important in Brazil, where only 11 species were observed in the canopy (8% of all core canopy species), and none of the top 20 species were

TABLE 3.6. Observed vs. expected (95% confidence interval) species richness of feeding guilds and edge species in the canopy assemblages of Honduras and Brazil. Expected values were derived from random draws from regional species pools in each country. Cases when observed species richness is significantly greater or less than expected values are indicated by "<" and ">" respectively. Note in particular the prevalence of omnivores.

	Honduras			Brazil		
Comparison	No. species observed	Sig.	No. species expected	No. species observed	Sig.	No. species expected
Guilds						
Insectivore	18		17-30	23	<	33-49
Frugivore	5		2-10	11		7-18
Granivore	2		0-5	11	>	2-9
Nectarivore	8		1-9	7		2-9
Raptor	1	<	2-10	11		5-14
Omnivore	32	>	18-31	45	>	27-41
Edge species	16	<	17-29	14	<	21-35

TABLE 3.7. Distribution of canopy bird species in Pico Bonito National Park, Honduras, and Manaus, Brazil, by residency status.

Residency Status	No. species (% of total)	
	Honduras	Brazil
Breeding Residents	89 (75)	134 (92)
Migrants	29 (25)	11 (8)
Nearctic	24 (20)	4 (3)
Resident	19 (16)	4 (3)
Transient	5 (4)	-
Austral	1 (1)	3 (2)
Also Breeding	-	2 (1)
Austral + Nearctic	-	1 (1)
Austral + Nearctic + Resident	-	1 (1)
Elevational	2 (2)	-
Vagrants	2 (2)	-
Total no. species	118	145

long-distance migrants. Brazil's 11 migrant species likewise did not differ from the null expectation.

DISCUSSION

Overview

Difficulty of access into the forest canopy has hindered the study of canopy bird assemblages as well as attempts to unify concepts on their structure and organization. The present study takes several steps to make such an attempt possible. First, I present a description of a canopy bird assemblage from northern Middle America, thereby broadening our perspective of canopy birds in lowland Neotropical rainforests. Second, I present a comparison of canopy bird assemblages from distant Neotropical forests, based on similar canopy-based censuses in Honduras and Brazil. These sites are particularly useful for such a comparison because they share similar climate and forest structure, yet offer relatively independent biogeographic histories, being separated by over 2000 km. Most importantly, I took three steps designed to clarify previously unresolved arguments on the composition of canopy bird assemblages: 1) by placing bird observations into distinct strata in Honduras I achieved a quantitative definition of the core canopy birds at that site; 2) I assessed the relative importance of dietary guilds and of edge and migrant species in Honduras and Brazil by comparing the observed composition of these groups with random expectations drawn from regional species pools; and 3) by reclassifying data sets from Costa Rica and Panama using similar criteria, I am able to make a unified comparison of bird assemblages of lowland Neotropical rainforest canopies.

Species Richness and Abundance

Forest bird-species diversity is notably higher in Amazonia than in Middle America at levels of both local (alpha) and regional (gamma) diversity (Karr et al. 1990, Terborgh et al. 1990, Blake 2007). For a majority of avian families, generic and species richness is also higher

in Amazonia. Despite these patterns, overall richness of the canopy assemblages did not differ significantly between Honduras and Brazil. If I include six species locally extirpated from the Honduras study site (*Ara macao, Amazona farinosa, A. autumnalis*) or reduced below detectable levels due to persecution (*Spizaetus ornatus, S. tyrannus, S. melanoleucus*), and four species observed in the canopy but outside standardized surveys (*Falco rufigularis, Pachyramphus major, Dendroica cerulea, Wilsonia canadensis*), the difference in observed richness is reduced further to only 17 species, a difference of 12% between sites. Given that overall richness of forest bird species is approximately 35% higher in Brazil, the similarity in bird-species richness in the forest canopy is striking. Higher richness of migrant species in Honduras, roughly three times greater than in Brazil, partially explains this finding. Especially notable was the greater richness in the family Parulidae, represented by 11 more species in Honduras than Brazil, and the families Tyrannidae, Vireonidae, and Cardinalidae, which together contained 15 migrant species. Additionally, the number of hummingbird species observed in the Honduras canopy was twice that as observed in Brazil (14 vs. 7 species), despite equal species richness at the regional level. I suspect that the high number of individual flowering trees in the Honduras canopy (principally *Vochysia guatemalensis* and *Symphonia globulifera*) may have attracted a greater diversity of hummingbird species into the canopy. During peak flowering, as many as eight individuals of seven species were observed in the canopy during a single 3-hr census, whereas in Brazil the median number of both species and individuals observed per census was one. This difference may be due to factors intrinsic to the Honduras site, because a similarly high richness of hummingbirds was not observed in Costa Rica (five species) or Panama (seven species).

Nonetheless, the added richness of migrants and hummingbirds for Honduras does not completely account for the similarity in species richness to Brazil. Clearly, a smaller proportion of regional forest species occurs in the canopy stratum in Brazil. One plausible explanation is

that differences in stratification result from the difference in taxonomic composition of the local avifaunas. At the Brazil site, the families Tinamidae, Cracidae, Furnariidae, Thamnophilidae, Formicariidae, Pipridae, and Troglodytidae, are all dominated by species of lower and middle forest strata, and richness of these families is more than double their richness in Honduras. In contrast, the few families with similar (Trochilidae, Vireonidae) or greater (Parulidae, Cardinalidae) species richness in Honduras are weighted with species of the upper forest strata, or with migrants, which seem to be more important locally in the canopy than at lower levels. Therefore, I suggest that taxonomic differences in the regional avifaunas explain in large part the patterns of similar richness between Honduras and Brazil canopies.

Despite similar species richness between Honduras and Brazil, patterns of species abundance differed markedly. My finding that the Middle American canopy was dominated by a few superabundant species and that species abundances were distributed more evenly in Amazonia are consistent with the findings reported by Robinson et al. (2000) for sites in Panama and Amazonian Peru. Robinson et al. described an "oligarchy" of eight common species, six from the understory and two from the canopy (*Hylophilus decurtatus* and *Zimmerius vilissimus*), that accounted for a disproportionate number (36%) of individuals at the Panama site. Likewise, in Honduras the seven most abundant canopy species each accounted for ≥ 4% of all canopy detections and a combined 46% of all canopy detections, whereas in Brazil only a single species reached comparable abundance. Finally, the overall pattern of more rare species than common ones observed in both the Honduras and Brazil canopies mirrors results from other lowland Neotropical forest sites (Pearson 1977, Karr et al. 1990, Terborgh et al. 1990, Thiollay 1994b, Robinson et al. 2000).

Migrant Richness

The importance of migrants in lowland Neotropical forest canopies deserves special

recognition. Even in Brazil, where a greater proportion of Austral to Nearctic migrants is observed, migrants are observed disproportionately more often in the canopy than in the understory (Bierregaard 1990, Stotz et al. 1992). Moreover, few migrant forest birds are true ground-dwellers, and the majority inhabits mid- to upper forest strata. Of 36 passeriform species that are long-distance migrants to the Honduras study site, only six occur principally on the ground or in the understory (*Seiurus noveboracencis*, *S. aurocapilla*, *S. motacilla*, *Oporornis formosus*, *Wilsonia citrina*, *Hylocichla mustelina*). Therefore, the annual influx of migrants to tropical forests adds disproportionately to the midstory and canopy. Finally, the pool of migrant species available to colonize the canopy in Honduras is substantially greater than in Brazil (Kelly and Hutto 2005), thereby disproportionately weighting the Honduras canopy with this group.

Trophic Organization

Little consensus has been reached on the trophic organization of bird assemblages in lowland Neotropical rainforest canopies. One confounding factor is that assignments to dietary guilds are not consistent among studies. In the Honduras canopy, omnivores and insectivores were dominant in terms of species richness, whereas omnivores dominated in terms of numerical abundance. When I reclassified species' assignments to dietary guilds from previous studies using similar criteria, and restricted analyses to true forest species by eliminating aerial foragers and scavengers, a similar pattern emerged for all four Neotropical sites studied thus far. In Costa Rica, Panama, and Brazil, omnivores and insectivores were the most species-rich groups, with slightly higher richness in the omnivore guild for three of four forests. Similarly, omnivores predominated in numerical abundance at all sites. In the understory of lowland Neotropical rainforests this patterns seems to be reversed. In Costa Rica insectivore species richness was three times greater than that of omnivores, and individual abundance of insectivores twice as

high (Blake and Loiselle 2001). In Brazil, 80% of individual abundance and 69% of the biomass of understory species were insectivores (Bierregaard 1990). The greater importance of omnivory in rain forest canopies contrasts with the greater predominance of insectivory in rain forest understories. This phenomenon may be related to the greater temporal and spatial unpredictability of canopy resources, which could favor diet generalists or vagile species like migrants able to take advantage of diverse resources over broad areas (Martin 1985).

Habitat Affiliations

Another topic that remains unsettled is whether lowland Neotropical rainforest canopies are dominated by species of edges, openings, and secondary habitats, as reported for Panama by Greenberg (1981), or forest species, as observed by Loiselle (1988) and Naka (2004). My analyses for Honduras and Brazil showed that edge species were underrepresented in the forest canopy at both sites when compared with the regional species pool available to colonize the canopy. I propose that the occurrence of edge species in the canopy in Panama was due to the location of the tower in young secondary forest and the proximity of forest openings. By comparison, Naka (2004) observed relatively more scrub species in the canopy surrounding the tower at Reserva Ducke, situated on the outskirts of Manaus and surrounded on three sides by open, agricultural and human-disturbed habitats, than at two towers in the midst of uninterrupted primary forest. Of further note, some of the most common species reported from the Panama canopy are commonly associated with gardens or forest edge habitats, notably *Coereba flaveola*, which was only rarely observed in the canopy in Brazil and never in Costa Rica or Honduras, despite being found in neighboring secondary forests and open habitats.

Core Species of Lowland Neotropical Rainforest Canopies

Many species occur in the forest canopy as occasional visitors from lower forest strata or vagrants from non-forest habitats, thus complicating a characterization of the core species of

lowland Neotropical rainforest canopies. Having quantified the core canopy species for Honduras and compensated for methodological differences in previous studies, I am able to present a broad-scale characterization of the constituent species in lowland Neotropical rainforest canopies. The species in the 26 genera that, at least historically, occurred at all sites should be taken as the nucleus of the core species most likely to be found in Neotropical canopies. The remaining 25 genera observed at a minimum of three sites complete the constituency of core canopy species. Some general observations on this group are worth noting. In terms of species richness, the Tyrannidae is the predominant family in the canopy, with twice as many species as any other family. Other important families include Thraupidae (18 species in the sample) and Psittacidae (nine species). Notwithstanding extirpations, the canopy typically includes seed predators that are large (*Ara*), medium (*Amazona*), and small (*Brotogeris*, *Pionus*). Although Neotropical forest raptors are diverse in size and diet, the medium-sized species in *Leucopternis* that prey largely on reptiles and amphibians (Thiollay 1994a) appear to represent the core carnivores of the canopy. The genus *Euphonia* is particularly well represented in the canopy, with approximately 30% of known species observed just in my sample.

In conclusion, although I was able to address previously unanswered questions about the structure and organization of canopy bird assemblages, much remains to be learned about this understudied group of birds. Given my experience with multiple survey methods for canopy birds I offer a few recommendations for future studies. As previously shown by Anderson (2009), ground methods alone are not adequate for canopy birds. I argue that the use of canopy-based methods at tropical field stations and other sites with continual scientific presence are essential for the accurate representation of long-term population trends, especially of secretive and rare or declining canopy species. Secondly, climbing a large number of trees is arduous, potentially dangerous, and time consuming. A small number of towers or carefully selected trees

interspersed throughout an area provides an excellent overview of local canopy dynamics and is a worthwhile tradeoff to climbing many trees.

CHAPTER 4: MORPHOMETRIC PATTERNS OF ECOLOGICAL ASSEMBLY IN A NEOTROPICAL BIRD ASSEMBLAGE

INTRODUCTION

A fundamental premise in ecology is that communities comprise subsets of species derived from larger pools of available species (Diamond and Case 1986, Weiher and Keddy 1999). The challenge for ecologists is to uncover the processes by which some available species become members of the community whereas others do not. Diamond (1975) hypothesized a series of assembly rules that governed the exclusion of certain species from 'forbidden combinations', a concept emphasizing the importance of interspecific competition and the limiting similarity of co-occurring species. An alternative concept is one of deletion (Keddy 1992), in which biotic interactions such as climatic conditions or disturbance regime act as biological filters that eliminate regional species from occurrence in a local community. The balance of these two processes, competitive interactions and environmental filtering, provide the backdrop for an apparent paradox in community ecology. On the one hand, environmental filtering should restrict community membership to similar species with ecologically constrained traits that benefit survival and fitness in a particular environment (Díaz et al. 1999, Mayfield et al. 2009). On the other hand, competitive exclusion should limit the similarity of co-occurring species (Levin 1970, Brown and Nicoletto 1991, Kelt and Brown 1999).

Morphological analyses are a powerful tool in making inferences on community structure and organization (Ricklefs and Miles 1994, Wainwright and Reilly 1994). Central to this approach is the premise that an organism's morphology in part determines its ecological niche, in particular its ability to detect, obtain, and process food, and its selection of microhabitats (Hutchinson 1957). Positions of species in morphological space are thus used to assess the predominance of deterministic processes in structuring ecological communities (Ricklefs and Travis 1980, Willig and Moulton 1989, Moreno et al. 2006). Competition and environmental

filtering make opposing predictions within this context. Based on competition theory, two or more species with sufficiently similar morphologies will compete for resources until character displacement or competitive exclusion are manifested (Gause 1934, Hutchinson 1959, MacArthur and Levins 1967). On the basis of competition theory, a prediction for community structure is one of morphological dissimilarity, manifested as overdispersion of species in morphological space (Schoener 1974, Ricklefs and Travis 1980, Moulton and Pimm 1986). Because environmental filtering works at the level of traits, we expect morphological similarity of species with optimal phenotypes for an environment, manifested as morphological underdispersion within a community (Cavender-Bares et al. 2004, Mayfield et al. 2009).

Avian assemblages in forest canopies are an appropriate system within which to study assembly mechanisms through the lens of morphometrics. In birds, the link between morphology and a species' ability to locate, capture and handle food, as well as its selection of microhabitats, is well documented (Fitzpatrick 1985, Moermond and Denslow 1985, Vanhooydonck et al. 2009). The utility of morphometric analyses in the study of community assembly in birds has also been established (Ricklefs and Travis 1980, Moulton and Pimm 1986). Further, the harsh environment of the forest canopy is thought to place a number of constraints on the movements and behavior of birds that potentially could exert a selective influence on morphological traits (Winkler and Preleuthner 2001, Walther 2002, Burney and Brumfield 2009).

A question of further interest that may be addressed on the basis of morphometric analyses is a long-standing paradox in tropical ecology concerning the annual integration of a large number of migrant birds into resident bird communities. Nearctic-Neotropical migrant birds spend up to seven months on tropical non-breeding grounds as part of their annual cycle. The annual arrival of these migrants, many of which are principally insectivorous, greatly

increases the number of birds in tropical habitats at a time of year when arthropod abundance is at its annual low (Janzen 1973, Hespenheide 1980, Greenberg 1995, Strong and Sherry 2000). The question that arises is how tropical bird communities accommodate a dramatic annual influx of potential competitors (Keast and Morton 1980). In light of numerous hypotheses concerning the availability of resources to migrant and resident insectivorous birds in tropical forests (Greenberg 1995, Johnson et al. 2006), morphometric analyses may aid in understanding the role that competition has played in structuring the assemblage of avian insectivores in tropical forests.

To test possible assembly mechanisms among forest canopy birds, I combine a year of fieldwork in Honduras in which I characterized the local forest bird community with linear measurements obtained from museum specimens. I follow Fauth (1996) in the use of the terms "community" (a set of species found together a common area), "assemblage" (phylogenetically related species together in a common area), and "ensemble" (phylogenetically related species exploiting similar resources in a common area) to differentiate groups with increasing likelihood for competitive interactions. I test for non-random patterns of community assembly by comparing the empirical values of morphometric dispersion from observed assemblages and ensembles with expected values derived from randomized resampling of larger species pools. Significant deviation from random patterns would be interpreted as evidence of ecological processes operating on community structure. I specifically test whether avian morphologies of observed assemblages and ensembles are significantly more over- or underdispersed than expected, and interpret the results in light of hypotheses concerning competitive interactions and environmental filtering outlined above.

METHODS

Study Site and Bird Censuses

Fieldwork was conducted in Pico Bonito National Park in northern Honduras from April

1996 to April 1997. A detailed description of the study site and field methods as well as analytical techniques are given in Anderson (2009). Briefly, I censused birds on a 100-ha study site in lowland Neotropical rainforest using multiple ground- and canopy-based methods. I placed bird observations into one of four forest strata (ground, understory, midstory, and canopy) and used the method of Neu et al. (1974) to quantify birds' preference for the canopy stratum. This allowed me to distinguish the core canopy birds of the study area (sensu Remsen 1994), defined as those species with a greater than expected frequency of observation in the canopy stratum (Haney and Solow 1992, da Silva et al. 1996), from the remainder of species observed in the canopy. I further characterized the canopy bird assemblage by assigning species to one of six major feeding guilds: insectivores, omnivores, frugivores, granivores, nectarivores, and raptors. Classification among guilds was based on published sources (Stiles and Skutch 1989, Robinson et al. 2000) as well as on personal observations.

Species

Any search for nonrandom morphometric patterns of community assembly must be made relative to an appropriate context within which the association between morphology and deterministic ecological processes can be weighed (Willig and Moulton 1989, Huston 1999). The identification of an appropriate context is subject to criteria regarding choice of species and choice of scale: species under consideration must be sufficiently similar as to belong to the same functional type, and the size of the area in which species will be considered must be small enough for ecological processes to exert an influence on the community under study (Schoener 1974, Willig and Moulton 1989, Huston 1999). To meet these criteria, I restrict analyses to species from the order Passeriformes that consume insects as a substantial portion of the diet (henceforth "insectivores", although this categorization includes species from the omnivore guild

that consume fruit and nectar as well as insects), and I consider only those species observed within the study area. Assignment to the insectivore ensemble is based on published sources (Stiles and Skutch 1989, Robinson et al. 2000, Fitzpatrick 2004) as well as personal observation. Within the study area I consider three levels of organization that are increasingly restrictive in membership and, therefore, likely to experience competition: community, assemblage, and ensemble. I define the local community as all avian insectivores observed in the study area. I used the level of community primarily as a species pool from which to construct null groupings of species and compare randomly derived morphometric values with those from observed assemblages and ensembles. The canopy assemblage was defined as all insectivores observed in the canopy, whereas the core canopy ensemble consisted of those insectivores defined as core canopy species (Anderson 2009). Species used in analyses are listed in the Appendix A.

Morphological Measures

I measured nine linear variables that represent the size and shape of major functional attributes of bird external anatomy likely to influence the selection and capture of insect prey as well as microhabitat use. I measured two wing variables: length of the longest primary and length of the first secondary. From these I calculated Kipp's index ($I_k = 100 \times \Delta S1/W$, in which $\Delta S1$ represents the distance from the first secondary to wing tip when the wing is folded and W is the length of the folded wing), a measure used commonly as a proxy for aspect ratio (Lockwood et al. 1998). Lengths of the inner and outer retrices were measured from the base of the central retrix pair. From tail measurements I calculated tail graduation (length of outer retrix subtracted from length of inner retrix, which yields a negative value for a forked tail, and a positive value for rounded or square tails). I measured length of the tarsometatarsus (henceforth "tarsus") as a measure of leg length, and length of the hind toe excluding the claw. Bill length from the anterior border of the nares to bill tip, and bill width and depth (vertically), also at the anterior

nares, described bill shape. All measurements were recorded to the nearest 0.1 mm. The seven measurements included in analyses were: Kipp's index, tail graduation, tarsus length, toe length, and bill length, width, and depth. Samples included three males and three females of each species, and six individuals of each sex in dimorphic species (*Psarocolius wagleri* and *P. montezuma*).

I measured study skins housed at the Louisiana State University Museum of Natural Science. I tried whenever possible to measure specimens belonging to the same subspecies as those constituting the insectivore ensemble of the Honduras canopy and that were collected in Honduras. When this was not possible, I selected specimens based on these criteria listed in decreasing order of importance: (1) specimens of the same subspecies collected outside Honduras; (2) specimens of a different subspecies collected in Honduras; (3) specimens collected in Middle America, principally southern Mexico, Belize, Costa Rica, and Panama.

Data Analyses

I describe morphometric patterns of community structure in canopy insectivores based on three approaches: (1) a characterization of the functional morphology of birds derived from principal components analysis (PCA); (2) the distribution of member species within morphological space; and (3) the morphometric volume occupied by member species. Data were first log-transformed to remove scaling artifacts associated with body size differences, and to more nearly equalize the variances of the measurements (Ricklefs and Travis 1980, Gotelli and Ellison 2004). Log-transformed morphometric values were averaged for each species.

I first described morphological variation of bird assemblages by means of a principal components analysis (Ricklefs and Travis 1980). Principal components were calculated from the covariance matrix, as opposed to the correlation matrix, for two reasons: (1) it preserves the relative scaling of points within morphometric space; and (2) it permits a direct interpretation of

the components' variances through use of eigenvalues (Ricklefs and Travis 1980, Lovette et al. 2002). Subsequent analyses characterizing the morphometric space occupied by bird assemblages or ensembles were based on principal component scores.

I used nearest-neighbor distances (NND) and minimum-spanning trees (MST) to assess the distribution of member species within the morphological space occupied by avian insectivores (Ricklefs and Travis 1980, Moreno et al. 2006). NNDs are based on Euclidian distances between pairs of species in a grouping and are used as a measure of species packing (Ricklefs and Travis 1980). MSTs are likewise based on Euclidian distances in the space formed by the seven morphological variables and are equal to the shortest series of n-1 segments connecting the n species in an assemblage (Moulton and Pimm 1986, Willig and Moulton 1989). The mean length of the connecting segments (henceforth MSTD) represents a measure of interspecific distance or species packing.

Volume of the morphometric space is compared separately on the basis of NND and MST approaches. For the NND approach, volume of the morphometric space is calculated as the product of the standard deviations of the principal components (Ricklefs and Travis 1980). For the MST approach, total length of the MST (henceforth MSTL) is used to quantify the volume of the morphological space (Moulton and Pimm 1986, Moreno et al. 2006). Because the PCA does not distort the morphological space, distance and volume calculations for both NND and MST approaches were based on principal components (Ricklefs and Travis 1980).

I decided a priori to use both NND and MST approaches based on the recommendation of Moreno et al. (2006), who observed that studies based on either NND or MST often provided contrasting results for the role of deterministic processes in structuring ecological communities. I concluded that the use of both approaches on a single system would allow a more robust interpretation of morphometric patterns observed in the current study.

Phylogenetic PCA

An important assumption of PCA is independence of data points. The purpose of phylogenetic PCA is to control for the expected covariances between morphometric values of individual taxa due to phylogeny and thereby fulfill this assumption. I used the methods for phylogenetic PCA proposed by Revell (2009) to correct for nonindependence among observations. The first step in phylogenetic PCA is to compute a matrix that describes the expected covariances of the data due to taxonomic relatedness. This error structure is calculated from an evolutionary hypothesis combined with an *n* x *m* data matrix containing the data for *m* traits measured in *n* species (Revell 2009). I estimated the phylogenetic hypothesis for the 71 avian insectivores observed in the Honduras canopy from gene sequences for the cytochrome b (cyt *b*), cytochrome oxidase I (COI), and recombination activating 1 (RAG-1) genes obtained from GenBank, and constructed the phylogeny using maximum likelihood. Sequences were not available for 12 species and I used two steps to estimate taxonomic relatedness for them. First, I substituted gene sequences of close relatives for 10 species (*Dendrocolaptes sanctihomae, Ornithion semiflavum, Mionectes oleagineus, Rhytipterna holerythra*, *Vireolanius pulchellu*s, *Polioptila plumbea, Cyanerpes lucidus, Psarocolius montezuma, Euphonia gouldi*, *Euphonia minuta*). For the remaining two species (*Hylophilus decurtatus*, *Ramphocaenus melanura*), taxonomic relationships were estimated by mapping the species by hand onto the existing tree. GenBank accession numbers, genes used for each species, and substitute species used in analyses are listed in the Appendix A. Although the phylogenetic tree (Appendix B) for the Honduras canopy assemblage is not 100% accurate for the reasons stated above, it is a sufficient approximation suitable for my primary objective: to control for taxonomic covariance among taxa and phenotypic traits and determine whether this covariance explained any of the morphometric patterns observed for canopy birds.

Statistical Significance and Randomizations

I used a randomization procedure to construct expected groupings of insectivores and compare the morphometric values of dispersion and volume of these with empirical values calculated for real ensembles and assemblages. Specifically, I drew at random and without replacement from a larger species pool a number of species equal to that in the corresponding observed grouping, calculated values of the morphometric space occupied by the random grouping, and repeated this process 5,000 times to construct 95% confidence limits defining the null hypothesis.

Species Pools

Defining appropriate species pools is one of the most important procedures when testing for non-random patterns of community organization (Huston 1999, Kelt and Brown 1999). Species should belong to the same functional type, and be restricted in occurrence to the same time and place, prerequisites for ecological structuring forces to act with sufficient frequency and intensity to produce recognizable patterns of community organization (Moulton and Pimm 1986, Huston 1999). My largest species pool from which species were randomly drawn consisted of all avian insectivores observed in the canopy of the study area. During randomizations I further grouped species into three levels of organization based on the inclusion or exclusion of migrant insectivores. In the first, empirical values for resident-only species ensembles were compared with expectations drawn from combined resident and migrant species pools. This comparison was designed to test for differences in ecomorphological patterns between the resident insectivore ensemble and the combined resident+migrant ensemble. The second class of tests compared empirical values from resident-only ensembles and larger resident-only species pools, whereas the third class compared empirical values from combined resident-migrant ensembles with expectations from larger resident-migrant species pools. These two classes of

randomizations were designed to test whether ecomorphological patterns of real insectivore ensembles and assemblages deviated significantly from random patterns. I refer to these latter classes of randomizations with similar structure as balanced randomizations. Finally, the two species in the genus *Psarocolius* were dramatically larger than the majority of the remaining species. Suspecting that their inclusion in analyses might affect the morphological characterization of the insectivore ensemble, I ran PCAs in which *Psarocolius* spp. were alternately included or excluded.

Three possible outcomes can result from the randomization procedure: empirical value < expected value, empirical value > expected value, and empirical value ~ expected value, or no significant difference between empirical and expected values. If insectivore assemblages and ensembles were randomly assembled, then I would expect empirical values for NND and volume to fall within the 95% confidence limits obtained from randomizations. Significant differences between empirical and expected values can be interpreted as biologically meaningful deviations from random, thereby suggesting the operation of deterministic assembly mechanisms. All statistical tests and randomizations were conducted in R (R Development Core Team 2008) with code written by J. S. Tello.

RESULTS

I obtained morphological measures from 426 individuals of 71 species of avian insectivores pertaining to 13 families. I treated males and females of two dimorphic species (*Psarocolius wagleri* and *P. montezuma*) as distinct "taxa," for a total of 73 taxa. More information on individual species' abundances on the study area is found in Chapter 3.

The shape and dimensions of the morphological spaces occupied by the 71 canopy species and 47 core canopy species are revealed by the principal components analysis (Table 4.1). Results for all canopy species and core canopy species are shown separately because these

TABLE 4.1. Principal components analysis of morphometric variables from avian insectivores of the rain forest canopy, Honduras. Factor loadings and proportion of the variance explained by each component are shown.

	Component						
Variable (log_{10})	I	II	III	IV	V	VI	VII
Core canopy species							
Kipp	-0.035	0.399	0.885	0.098	0.206	-0.048	0.050
Graduation	0.487	-0.734	0.242	0.131	0.372	-0.056	0.081
Tarsus	0.319	-0.044	0.168	0.172	-0.563	-0.249	-0.678
Toe	0.322	0.030	0.089	0.097	-0.610	-0.022	0.711
Bill length	0.499	0.214	0.001	-0.834	0.075	0.009	-0.057
Bill width	0.331	0.397	-0.318	0.316	0.330	-0.644	0.094
Bill Depth	0.446	0.308	-0.146	0.372	0.123	0.719	-0.119
Variance explained							
percent	0.682	0.201	0.061	0.023	0.017	0.006	0.003
cumulative	0.682	0.884	0.945	0.974	0.990	0.997	1.000
				Component			
	I	II	III	IV	V	VI	VII
All canopy species							
Kipp	-0.061	-0.387	-0.895	-0.096	0.177	-0.055	0.045
Graduation	0.525	0.726	-0.266	-0.192	0.279	-0.046	0.100
Tarsus	0.297	-0.030	-0.103	-0.198	-0.545	-0.386	-0.644
Toe	0.287	-0.116	-0.046	-0.170	-0.631	0.076	0.685
Bill length	0.516	-0.166	-0.056	0.836	0.007	0.052	-0.040
Bill width	0.319	-0.400	0.303	-0.210	0.407	-0.625	0.211
Bill Depth	0.428	-0.348	0.142	-0.378	0.171	0.668	-0.238
Variance explained							
percent	0.623	0.246	0.067	0.032	0.021	0.007	0.004
cumulative	0.623	0.869	0.935	0.967	0.989	0.996	1.000

form the basis for subsequent analysis on the dispersion of species in morphological space; however, I restrict the qualitative description of morphometric space to the primary group of interest, the core canopy species. Similarly, the inclusion of *Psarocolious* spp. did not affect the characterization of the insectivore ensemble and results presented here include males and females as separate taxa. The first principal component measures overall size, based on the positive and high values for all but one of the seven axes (Table 4.1). Species having the extreme values on this component weigh 44 to >400 g at one extreme (*Xiphorhynchus flavigaster, Cyanocorax morio*, *Psarocolius* spp.) and 8-12 g at the other (*Ornithion semiflavum*, *Vermivora peregrina*, *Contopus* spp.). PC I accounts for 68% of the total variance in morphological space. Factor loadings indicate that PC II (20% of the variance) separates species based on tail shape, wing shape, and bill shape. At one end of the component are species with graduated tails, long narrow bills, and rounded wings (*Thryothorus maculipectus, Polioptila plumbea*, *X. flavigaster*), and at the other end are species with forked to square tails, wide or stout bills, and pointed wings (*Contopus sordidulus*, *Megarynchus pitangua*, *Myiodynastes luteiventris*). PC III accounts for 6% of the variance and is based on the ratio of bill width/wing shape. This axis separates species with wide bills and rounded wings (*Caryothraustes poliogaster, M. pitangua, Vireolanius pulchellus*) from those with narrow bills and pointed wings, largely warblers and vireos (*Mniotilta varia, Dendroica* spp., *Vireo flavifrons*). The remaining four principal components (IV-VII) account for only 5% of the total variance and are excluded from further consideration.

Few migrant species are segregated on the basis of PC I and PC II (Fig. 4.1a). The morphometric space occupied by residents and defined by these two axes contains all but four of the core canopy migrant species. PC III segregates 12 of 20 migrant species (55%) from the core canopy residents, and four of the remaining eight migrant species included in the resident

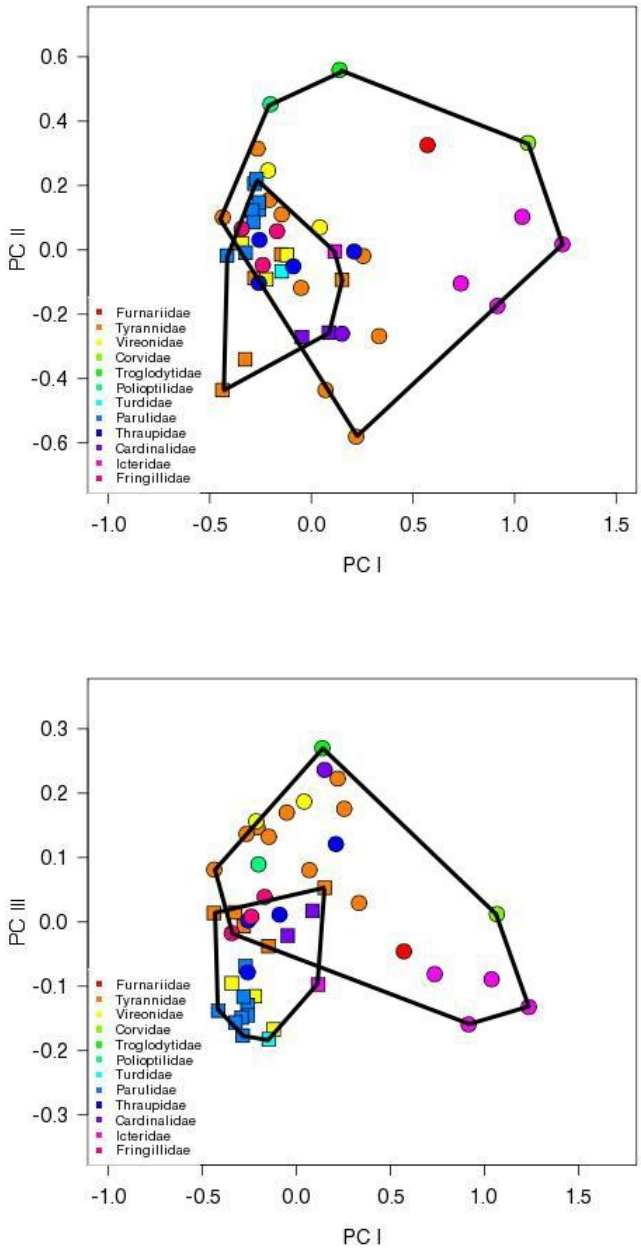


FIGURE 4.1. Plots of principal component scores describing morphometric variation of core canopy avian insectivores. PC I represents overall body size. PC II is associated with species with graduated tails, long, narrow bills, and rounded wings (positive scores), or species with forked to square tails, wide or stout bills, and pointed wings (negative scores). PC III is associated with species with wide bills and rounded wings (positive scores) or narrow bills and pointed wings (negative scores). Circles and squares represent resident and migrant species, respectively.

morphospace occur at the edge of the volume circumscribed by principal components I and III (Fig. 4.1b). Migrant insectivores seem to differ from resident insectivores largely on the basis of bill and wing shape.

Results from standard PCA indicate that canopy insectivores shared greater morphological similarity than expected by chance. Empirical values for NND and MSTD were significantly smaller ($P<0.05$) than expected values in all analyses (Table 4.2, contrasts1-4). Similarly, empirical values for volume were significantly smaller than expected values for a majority of contrasts (Table 4.2, contrasts 1-4). In a single contrast (Table 4.2, contrast 3), empirical NND volume was significantly greater than expected volume, even though interspecies distances were smaller, and empirical MSTL volume was smaller than the expected volume. I interpret this seemingly contradictory result as a mathematic artifact of the randomization process, as follows. Migrants occupy a smaller morphospace than do residents (Fig. 4.1a, b). During randomizations, the chance that a selected migrant will be morphologically similar to a resident species is greater than the chance that a resident will be similar to another resident, because the overall dispersion of residents is greater. A visual interpretation of the morphospace (Fig. 4.1) indicates that combined resident+migrant volume is larger, not smaller, than the resident-only volume. It appears more likely that the inclusion of migrants in the canopy insectivore assemblage dilutes the pattern of morphological similarity found in the residents-only ensemble.

Results from phylogenetic PCA indicated that the morphology of canopy insectivores did not differ from a random expectation (Table 4.2, contrasts 5-8).

DISCUSSION

Non-random patterns of local co-existence of species have long been of interest to ecologists (Diamond 1975). Interest in such patterns led to the term ‘assembly rules,’ which can

TABLE 4.2. Pairwise contrasts of empirical values (E) and expected values (N) describing attributes of morphometric space occupied by avian insectivores and defined on the basis of principal components analysis (PCA). Metrics for morphometric space include interspecific distances, and volume of the space occupied by member species. Differences between empirical and expected values (E<N and E>N) are deemed significant when an empirical value falls below or above 95% of the values derived from randomizations; otherwise contrasts are considered not significantly different (nd). Results from standard PCA and phylogenetic PCA are shown separately.

			Distance[b]		Volume[c]	
Contrast	Empirical group[a]	Null group	NND	MSTD	NNDV	MSTL
	Standard PCA					
1	core canopy res.	canopy res.	E<N	E<N	E<N	E<N
2	core canopy res.+mig.	canopy res.+mig.	E<N	E<N	nd	E<N
3	canopy res.	canopy res.+mig.	E<N	E<N	E>N	E<N
4	core canopy res.	core canopy res.+mig.	E<N	E<N	nd	E<N
	Phylogenetic PCA					
5	core canopy res.	canopy res.	nd	nd	nd	nd
6	canopy res.+mig.	canopy res.+mig.	nd	nd	nd	nd
7	canopy res.	canopy res.+mig.	nd	nd	nd	E>N
8	core canopy res.	core canopy res.+mig.	nd	nd	nd	nd

[a]res., resident avian insectivores; mig., migrant avian insectivores
[b]NND, nearest neighbor distances; MSTD, minimum spanning tree distances
[c]NNDV, nearest neighbor distance volume; MSTL, length of minimum spanning trees

be applied either to observed non-random patterns of community structure, or the mechanisms behind them (Weiher and Keddy 1999). The challenge in ecology is linking mechanism to pattern, for it is common for alternative but not mutually exclusive hypotheses to offer potential explanations for observed patterns (Stevens and Willig 1999, 2000).

One of the most often-cited assembly rules is morphological overdispersion resulting from interspecific competition for limiting resources (Moulton and Pimm 1986, Ricklefs and Miles 1994, Stevens and Willig 1999, Moreno et al. 2006). If we assume that competition will be most severe between similar organisms, then competition offers a parsimonious explanation for dissimilar morphologies among potential competitors (Kelt and Brown 1999). When analyzing morphometric patterns of canopy insectivores, I observed the opposite pattern, namely that species appeared underdispersed when compared with null expectations drawn from the larger species pool comprised of all avian insectivores observed in the forest canopy. Hyperdispersed morphological patterns are common but not ubiquitous in communities (Stevens and Willig 1999), and multiple hypotheses offer potential explanations for not finding such a pattern. First, competition may not have been intensive or extensive enough to involve the majority of species, cause local extinctions, or thereby exert a perceptible force on community structure (Moulton and Pimm 1986). Birds of tropical forest canopies are characterized by high vagility, which could be an adaptation to locating temporally and spatially variable food resources in the canopy (Martin 1985, Levey 1988, Levey et al. 1994, Johnson and Sherry 2001); this mobility may minimize temporal interactions of competitors and reduce the influence of competition (Moulton and Pimm 1986). For this reason the seasonal occurrence of migrants may actually dilute the mechanistic effect of competition within the resident canopy bird assemblage. Environmental variability, such as that found in the forest canopy, may also reduce the prevalence of competition as a structuring force. Morphological hyperdispersion is expected to

result only from competition that is both intensive and persistent, yet environmental variability may prevent a community from reaching a state of competitive equilibrium needed for morphological hyperdispersion to develop or persist (Moulton and Pimm 1986, Stevens and Willig 1999). Second, hyperdispersion of morphological patterns can be manifested two ways, through the deterministic effect of size assortment manifested at the community level, as tested in this study, or through size adjustment, a stochastic effect involving evolutionary shifts of morphological characters (Willig and Moulton 1989, Stevens and Willig 1999). Finally, competitive interactions may structure communities through non-morphological patterns, such as behavioral segregation (MacArthur 1958) or abundance patterns (Moulton and Pimm 1986, Stevens and Willig 2000).

Despite the potential for any of these a posteriori explanations to account for the morphological underdispersion I found, environmental filtering must also be considered as an ecological force potentially responsible for this pattern. Environmental filtering may be thought of as a restrictive force that limits community membership to similar species with ecologically constrained traits that allow survival or enhance fitness under a given set of abiotic or biotic conditions (Kembel and Hubbell 2006). Inasmuch as a local community is considered a subset of a larger regional pool of potential members (Diamond 1975, Kelt and Brown 1999), then environmental filtering acts as a force that deletes potential members ill-suited to local conditions. Because environmental filtering operates on traits rather than taxa, one prediction of environmental filtering is greater phenotypic similarity than expected by chance among members of a community (Weiher and Keddy 1995, Díaz et al. 1999, Mayfield et al. 2009). The canopy environment, distinct from and generally considered to be biotically and abiotically more severe than the relatively sheltered forest interior, may act as such a filter. The canopy is exposed to direct solar radiation and wind turbulence, and as such is subject to pronounced diurnal

fluctuations in temperature and relative humidity, as well as experiencing a high rate of evapotranspiration (Shaw et al. 2002, Madigosky 2004). Water potential, necessarily a function of gravity and tree height (Koch et al. 2004), is subject to dramatic seasonal fluctuations. This combination of factors produces heterogeneous patterns of resource availability in the canopy (Frankie et al. 1974, Levey et al. 1994, Levey and Stiles 1994, Foster 1996). Niche assembly, a product of environmental filtering, is expected to predominate in severe environments where species' abilities to persist in a locality are determined by their traits (Chase 2007). Where harsh conditions predominate, a large proportion of the regional species pool is eliminated, leading to higher similarity within the realized pool of the species that remain (Díaz et al. 1999, Mayfield et al. 2009). Environmental filtering, therefore, offers one parsimonious hypothesis for the underdispersed morphological pattern in canopy insectivores observed in this study.

Of additional interest are the community attributes that allow the large annual influx of avian insectivores into the resident bird communities of tropical forests. Various authors (Hutto 1980, Skutch 1985, Greenberg 1995, Johnson et al. 2005) have proposed mechanisms with the potential to have reduced competition among resident and migrant insectivores and facilitated the evolution of this phenomenon. Results from randomizations, in which no evidence of competition as a structuring force was found, would support this argument. Further, distributions of migrant and resident species in principal component space seem to indicate that the two groups differ in important morphological attributes related to feeding. This conclusion is further supported by the findings of Johnson and Sherry (2001) in which the distribution of wintering Neotropical migrants in Jamaica was not influenced by the distribution or abundance of resident avian insectivores.

Although environmental filtering offers a plausible explanation for the pattern of underdispersed morphologies observed, the importance of phylogenetic relationships underlying

this pattern must also be stated. After I controlled for the covariance associated between traits and taxa due to phylogeny, no morphometric patterns were discernable. Two possible interpretations exist for this finding. First, a strictly phylogenetic viewpoint would hold that no morphometric pattern exists among the canopy birds studied and that any similarity in phenotypes was simply an artifact of taxonomic relationships among canopy-living birds. I consider this conclusion untenable. In light of the recurring pattern revealed for interspecific distances and volume, as detected in both NND and MST approaches, the conclusion that core canopy birds represent a non-random association of species drawn from the larger canopy pool is a strong one. I propose that the co-occurrence of ecologically similar species in the forest canopy may represent a balance between environmental filtering and phylogenetic niche conservatism. The concept that species evolve within communities, and that community structure is simultaneously affected by phylogenetic and ecological processes, is increasingly appreciated (Cavender-Bares et al. 2006, Lovette and Hochachka 2006). In the case of canopy birds, filtering of species that can persist under the abiotic and biotic conditions in the canopy may favor certain clades of species over others.

Nonetheless, for reasons outlined above, it is premature to either invoke the predominance of any single process as having guided the assembly of the canopy insectivore assemblage, or to eliminate from consideration important processes, notably competition. Further testing of a more exhaustive set of alternative hypotheses (Krebs 1985) would add resolution toward understanding the processes responsible for community structure. Phylogenetic methods would be of particular interest in identifying taxonomic patterns of ecological co-existence of species (Webb et al. 2002, Cavender-Bares et al. 2004).

CHAPTER 5: CONCLUSIONS

An important goal in ecology has been to link patterns of community structure with mechanistic processes responsible for their origin. Interest in this realm has led to the term "assembly rules," which has been proposed to refer either to observed non-random patterns of community structure, or the mechanisms that produce them (Weiher and Keddy 1999). To this aim, researchers have employed a variety of approaches to test for non-random patterns of community structure, of which one, morphometric analyses, is the subject of this dissertation. In particular, I focused on the assemblage of canopy birds I observed in a lowland tropical rainforest in Honduras. Because canopy birds are poorly known in general, however, I began with the prerequisite steps of first testing methods for the study of canopy birds, followed by a comparison of canopy bird assemblages at distant sites in search of interesting patterns of community structure, before proceeding to analyses of non-random community structure and its possible origin in this group.

In Chapter 2 I compared three census methods for birds inhabiting the canopy of tall and structurally complex lowland rainforests. Two canopy-based methods were compared with ground-based point counts, a universally applied method for the censusing of forest birds. Although few notable differences were observed between canopy methods, results between canopy- and ground-based methods differed dramatically. On the basis of my results, I conclude that a reliance on ground-based methods for canopy birds in tropical forests will result in severe miscalculations of species richness and density at the level of both community and family, a misrepresentation of important ecological processes such as seed dispersal, and could negatively affect conservation practices in tropical forests. I propose that any tropical forest site possessing tall and complex forests, and of heightened biological interest or importance, should include regular canopy-based surveys in its monitoring program.

To document recurring patterns of community structure in canopy bird assemblages in Neotropical forests, I took a comparative approach in which I examined the birds inhabiting distant rainforest canopies in Middle and South America. I chose two sites in Pico Bonito National Park, Honduras, and Manaus, Brazil, with similar biotic and climatic environments yet separated by over 2000 km and differing in their respective biogeographic histories. I observed similar species richness in the canopy at both sites, despite higher forest bird richness in Brazil and underlying differences in the abundance distributions of species, which was demonstrably more even for the Brazil assemblage. In light of their differing biogeographic histories and underlying differences in species richness at the familial level, similarities in a number of community attributes are of interest. First, canopy bird assemblages in Honduras and Brazil were dominated by forest rather than edge species, as previously suggested (Greenberg 1981). Second, diet generalists dominated the canopy in terms of species richness and abundance, a pattern that recurred in Panama (Greenberg 1981) and Costa Rica (Loiselle 1988) after I standardized the results from these studies. Finally, the composition of dietary guilds in the Honduras and Brazil canopies was indistinguishable, a fact made more salient when dramatic differences in the familial composition of all forest birds at the respective sites is considered. I tentatively propose that the unique and harsh biotic and abiotic conditions in the forest canopy act as a selective mechanism that homogenizes avian assemblages in the canopy stratum.

To further explore patterns of community structure in canopy bird assemblages, and make inferences on mechanisms that could have produced such structure, I examined morphometric patterns of community assembly. In particular, I tested whether morphologies of core canopy birds, those species most characteristic of the canopy, represented a non-random draw of the available pool of species inhabiting the surrounding canopy. Two predictions formed the basis of randomizations. From competition theory, co-occurring species should be

less similar than expected by chance, whereas greater than expected similarity could result from environmental filtering selecting for species with optimal phenotypes for a unique or particularly harsh environment (Schoener 1974, Moulton and Pimm 1986, Mayfield et al. 2009). My results supported the latter thesis: core canopy birds were consistently underdispersed in morphometric space when compared to the dispersion of randomly drawn groupings of canopy birds. This finding was complicated, however, by the taxonomic relatedness of the species under consideration. When I controlled for the covariances between morphometric values of individual taxa due to phylogeny, no pattern of community assembly was detected. I conclude that the observed pattern of phenotypic similarity of core canopy species is real, that environmental filtering offers one parsimonious explanation for the pattern, and that this pattern has an underlying component related to phylogenetic history, as potentially explained by phylogenetic niche conservatism (Cavender-Bares et al. 2006, Lovette and Hochachka 2006).

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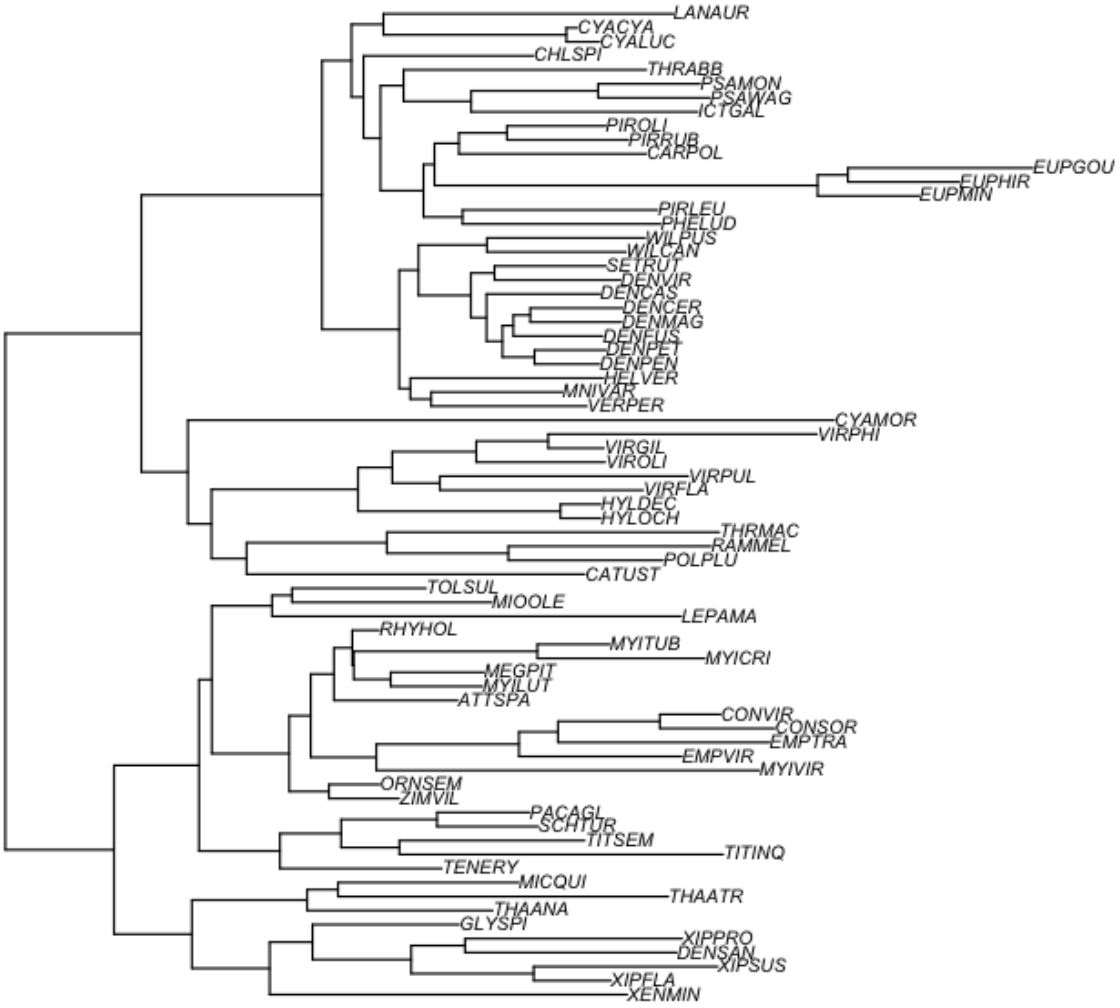
APPENDIX A - LIST OF TAXA AND GENBANK ACCESSION NUMBERS FOR GENES USED IN MORPHOMETRIC ANALYSES

Family and species	Canopy Status	Genes/ accession numbers: cyt *b*	COI	RAG-1	Substitute species
Furnariidae					
Xenops minutus	canopy	AY590050			
Glyphorynchus spirurus	canopy	AY089806		FJ461160	
Xiphocolaptes promeropirhynchus	canopy	AY089798			
Dendrocolaptes sanctithomae	canopy	EF212895		FJ461166	*D. certhia* (RAG-1)
Xiphorhynchus susurrans	canopy	AY089800			
Xiphorhynchus flavigaster	core	AY089799			
Thamnophilidae					
Thamnophilus atrinucha	canopy	EF030323			
Thamnistes anabatinus	canopy	EF639989		FJ461180	
Microrhopias quixensis	canopy	EF639960		FJ461187	
Tyrannidae					
Ornithion semiflavum	core			FJ501697	*O. inerme*
Myiopagis viridicata	canopy	AF453806	EU232809		
Mionectes oleagineus	core	DQ294509		FJ501669	*M. striaticollis* (RAG-1)
Leptopogon amaurocephalus	canopy	AF453808	EU232877		
Zimmerius vilissimus	core			FJ501772	
Tolmomyias sulphurescens	core		EU232855	FJ501757	
Terenotriccus erythrurus	canopy	DQ294529		FJ501753	
Contopus sordidulus	canopy	AF447608	DQ432862		
Contopus virens	canopy	AF447610	DQ432863		
Empidonax virescens	core	AY143205	AY666182		
Empidonax traillii	core	AY143202			
Attila spadiceus	core		EU232902	FJ501603	

Rhytipterna holerythra	canopy			FJ501739	*R. simplex*
Myiarchus tuberculifer	core		DQ433035		
Myiarchus crinitus	core		AY666501		
Megarynchus pitangua	core	EU442334	EU232917	FJ501668	
Myiodynastes luteiventris	core		DQ433836	FJ501677	
Schiffornis turdina	canopy	EF458547		FJ501743	
Pachyramphus aglaiae	canopy		DQ433057	FJ501700	
Tityra semifasciata	core	EF212894		FJ501754	
Tityra inquisitor	canopy	AF123643			
Vireonidae					
Vireo flavifrons	core	AF081962			
Vireo gilvus	canopy	AY030111			
Vireo philadelphicus	core	VPU12297			
Vireo olivaceus	core	X74260			
Hylophilus ochraceiceps	canopy	AY030109			
Hylophilus decurtatus	core				none
Vireolanius pulchellus	core	AF081959			*V. leucotis*
Corvidae					
Cyanocorax morio	core	EU442338			
Troglodytidae					
Thryothorus maculipectus	core	AY352546			
Polioptilidae					
Ramphocaenus melanurus	canopy				none
Polioptila plumbea	core	AY352535			*P. caerulea*
Turdidae					
Catharus ustulatus	core	AY049507		AY443265	
Parulidae					
Vermivora peregrina	core	AY216809			
Dendroica petechia	core	AF382996			
Dendroica pensylvanica	core	AY216828			
Dendroica magnolia	core	AY216837			
Dendroica virens	core	AY216841			
Dendroica fusca	canopy	AY340208			
Dendroica castanea	core	AY216835			

Dendroica cerulea	canopy	EU815676	
Mniotilta varia	core	AF383006	
Setophaga ruticilla	core	AF383008	
Helmitheros vermivorum	canopy	AF383004	
Wilsonia pusilla	canopy	AY216865	
Wilsonia canadensis	canopy	AF383016	
Thraupidae			
Lanio aurantius	core	EF529962	
Chlorophanes spiza	core	AF006215	
Cyanerpes lucidus	core	AF006225	*C. caeruleus*
Cyanerpes cyaneus	core	EF529958	
Cardinalidae			
Piranga rubra	core	AY955196	
Piranga olivacea	core	AF006248	
Piranga leucoptera	canopy	EF529999	
Thraupis abbas	canopy	EF529969	
Caryothraustes poliogaster	core	EF530022	
Pheucticus ludovicianus	canopy	AF447373	
Icteridae			
Icterus galbula	core	AY607656	
Psarocolius wagleri	core	AF472368	
Psarocolius montezuma	core	AY117698	*P. viridis*
Fringillidae			
Euphonia hirundinacea	core	EU442333	
Euphonia gouldi	core	AF383014	*E. fulvicrissa*
Euphonia minuta	core	AF006232	*E. laniirostris*
Crypturellus undulatus	outgroup		

APPENDIX B – PHYLOGENY FOR 71 SPECIES OF AVIAN INSECTIVORES DETECTED IN THE HONDURAS CANOPY



Species acronyms:

Acronym	Family	Species
ATTSPA	Tyrannidae	*Attila spadiceus*
CARPOL	Cardinalidae	*Caryothraustes poliogaster*
CATUST	Turdididae	*Catharus ustulatus*
CHLSPI	Thraupidae	*Chlorophanes spiza*
CONSOR	Tyrannidae	*Contopus sordidulus*
CONVIR	Tyrannidae	*Contopus virens*
CYACYA	Thraupidae	*Cyanerpes cyaneus*
CYALUC	Thraupidae	*Cyanerpes lucidus*
CYAMOR	Corvidae	*Cyanocorax morio*
DENSAN	Furnariidae	*Dendrocolaptes sanctithomae*
DENCAS	Parulidae	*Dendroica castanea*
DENCER	Parulidae	*Dendroica cerulea*

DENFUS	Parulidae	*Dendroica fusca*
DENMAG	Parulidae	*Dendroica magnolia*
DENPEN	Parulidae	*Dendroica pensylvanica*
DENPET	Parulidae	*Dendroica petechia*
DENVIR	Parulidae	*Dendroica virens*
EMPTRA	Tyrannidae	*Empidonax traillii*
EMPVIR	Tyrannidae	*Empidonax virescens*
EUPGOU	Fringillidae	*Euphonia gouldi*
EUPHIR	Fringillidae	*Euphonia hirundinacea*
EUPMIN	Fringillidae	*Euphonia minuta*
GLYSPI	Furnariidae	*Glyphorynchus spirurus*
HELVER	Parulidae	*Helmitheros vermivorum*
HYLDEC	Vireonidae	*Hylophilus decurtatus*
HYLOCH	Vireonidae	*Hylophilus ochraceiceps*
ICTGAL	Icteridae	*Icterus galbula*
LANAUR	Thraupidae	*Lanio aurantius*
LEPAMA	Tyrannidae	*Leptopogon amaurocephalus*
MEGPIT	Tyrannidae	*Megarynchus pitangua*
MICQUI	Thamnophilidae	*Microrhopias quixensis*
MIOOLE	Tyrannidae	*Mionectes oleagineus*
MNIVAR	Parulidae	*Mniotilta varia*
MYICRI	Tyrannidae	*Myiarchus crinitus*
MYITUB	Tyrannidae	*Myiarchus tuberculifer*
MYILUT	Tyrannidae	*Myiodynastes luteiventris*
MYIVIR	Tyrannidae	*Myiopagis viridicata*
ORNSEM	Tyrannidae	*Ornithion semiflavum*
PACAGL	Tyrannidae	*Pachyramphus aglaiae*
PHELUD	Cardinalidae	*Pheucticus ludovicianus*
PIRLEU	Cardinalidae	*Piranga leucoptera*
PIROLI	Cardinalidae	*Piranga olivacea*
PIRRUB	Cardinalidae	*Piranga rubra*
POLPLU	Polioptilidae	*Polioptila plumbea*
PSAMON	Icteridae	*Psarocolius montezuma*
PSAWAG	Icteridae	*Psarocolius wagleri*
RAMMEL	Polioptilidae	*Ramphocaenus melanurus*
RHYHOL	Tyrannidae	*Rhytipterna holerythra*
SCHTUR	Tyrannidae	*Schiffornis turdina*
SETRUT	Parulidae	*Setophaga ruticilla*
TENERY	Tyrannidae	*Terenotriccus erythrurus*
THAANA	Thamnophilidae	*Thamnistes anabatinus*
THAATR	Thamnophilidae	*Thamnophilus atrinucha*
THRABB	Cardinalidae	*Thraupis abbas*
THRMAC	Troglodytidae	*Thryothorus maculipectus*
TITINQ	Tyrannidae	*Tityra inquisitor*

TITSEM	Tyrannidae	*Tityra semifasciata*
TOLSUL	Tyrannidae	*Tolmomyias sulphurescens*
VERPER	Parulidae	*Vermivora peregrina*
VIRFLA	Vireonidae	*Vireo flatirons*
VIRGIL	Vireonidae	*Vireo gilvus*
VIROLI	Vireonidae	*Vireo olivaceus*
VIRPHI	Vireonidae	*Vireo philadelphicus*
VIRPUL	Vireonidae	*Vireolanius pulchellus*
WILCAN	Parulidae	*Wilsonia canadensis*
WILPUS	Parulidae	*Wilsonia pusilla*
XENMIN	Furnariidae	*Xenops minutus*
XIPPRO	Furnariidae	*Xiphocolaptes promeropirhynchus*
XIPFLA	Furnariidae	*Xiphorhynchus flavigaster*
XIPSUS	Furnariidae	*Xiphorhynchus susurrans*
ZIMVIL	Tyrannidae	*Zimmerius vilissimus*

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VITA

David L. Anderson was born in 1966 in San Bernardino, California, to Sally and Larry Anderson. Until the age of 14 he lived in San Bernardino, where all his pastimes involved the outdoors: fishing, camping, and swimming throughout California and western states; and exploring the desert washes and foothills surrounding his home. In the summer of 1980 he moved with his mother to western Washington, where he attended Eastside Catholic High School in Bellevue, and where he continued his exploration of western forests and mountains, including an expedition with Outward Bound. Following high school he enrolled in the Wildlife Management Program at Humboldt State University, one of the major decisions with the greatest influence on his personality and philosophies toward education and nature. It was at Humboldt that David learned that the study of wildlife could become a profession, where his innate spirit of freedom was allowed to blossom in the accepting and open culture of Humboldt County, and where his education benefitted from interactions with his student peers and professors. During his undergraduate years he worked no fewer than eight seasonal wildlife jobs in three western states, before volunteering to serve in the Peace Corps from 1991-1993. There he served as a wildlands promoter in Honduras and became irrevocably hooked on tropical nature and living in developing countries. David earned his master's Degree at Boise State University in 1998, on the basis of 12 months of fieldwork in the Río Plátano Biosphere Reserve, Honduras, the most moving and inspirational experience in his life to date. It was at BSU that he met Yasmina Wong, who would become his life-long partner. He worked for the Idaho Department of Fish and Game from 1999 to 2003. His and Yasmina's son Eli was born an Idaho native on July 4, 2002. David entered the doctoral program at Louisiana State University in the fall of 2004 to continue studies on tropical birds.